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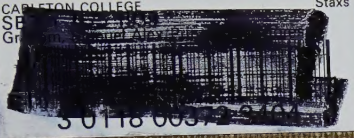

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Twenty feet in diameter and two hundred and fifty high, this giant sequoia has survived drought, fire, fungi, and insects. It has lived a thousand years in harmony with its associates, and bears mute testimony to what nature in her wisdom can produce under balanced conditions. The development of similar balances where insect outbreaks will seldom or never occur should be an objective of the forester.

(Frontispiece.)

PRINCIPLES

OF

FOREST ENTOMOLOGY

BY

SAMUEL ALEXANDER GRAHAM

Professor of Economic Zoology, University of Michigan
Collaborator, United States Department of Agriculture
Bureau of Entomology

SECOND EDITION

McGRAW-HILL BOOK COMPANY, INC.
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To

All Interested

in the Protection of Forests

and Forest Products

PREFACE

Any insect that feeds on trees is potentially a forest pest, and the number of these is legion. For instance, white oak alone provides food for more than 200 different species of insects. Fortunately only a very small proportion of all tree insects ever causes economically important damage. The rest are held down by environmental checks of one sort or another. When forest conditions are changed by such activities as logging, clearing for cultivation, road construction, grazing of wild or domestic animals, forest fires, wind throw, or the slower but no less certain changes resulting from plant succession, shifts occur both in the relative importance of the various natural checks and in the relative importance of the various forest insects.

Thus, as a result of changed conditions, some insects that were once common have now dropped into obscurity, whereas others that were once rare have become prominent pests. The truth of this statement is evident when we consider the pests of jack pine in the Lake states. Prior to 1920 this tree was usually considered to be especially free from insect enemies. But in 1923 extensive jack-pine forests were attacked and seriously injured by a combination of several insects. Among these were a sawfly then new to science, a moth that was known only as a pest of fir and spruce, a scale insect that was previously rare in collections, and a tussock moth that had seldom before been abundant.

Such shifts in the economic importance of species are not uncommon, and they make the problem of presenting the subject of forest entomology rather difficult. An adequate discussion of all tree species is impossible in a single volume of textbook length. If, on the other hand, the discussion is limited to the currently injurious species, changing conditions may soon make the selections economically obsolete.

In this book the subject of forest entomology is approached through a consideration of general underlying principles sup-

plemented by a study of certain insect species carefully selected to illustrate how these principles apply in individual instances. With this aim in view, a large proportion of this book is devoted to a discussion of these principles, especially from the ecological viewpoint. Examples of insects illustrating various ecological groups are discussed in more or less detail. These examples have been selected on the basis of their importance as pests. So far as possible, representatives from different parts of North America have been used. In many instances, other insects might be used as well as the one selected for illustration.

During the decade that has elapsed since the first edition of "Principles of Forest Entomology" was published there have been many advances in the field of forest entomology. Some investigations have provided new evidence substantiating accepted principles. Others have resulted in the modification of accepted concepts. Also, a number of new insect species, like the European pine-sawfly, have attained economic prominence as forest enemies and have been studied intensively.

In this revision the subject of forest entomology has been brought up to date. New information has been added concerning various forest insects, especially those that have recently become economically important. The chapter on Insect Abundance and the sections on termites and on bark beetles have been almost entirely rewritten in the light of recent information. The section dealing with insect-caused losses has been revised, using the most recent available data. Likewise, the more important recent publications have either been added to the bibliography or substituted for less satisfactory references.

As in the first edition, the objective of this revision is to present the subject of forest entomology from the forestry viewpoint. The emphasis is placed on the influence of insects on the forest rather than on the insects themselves. This is the chief reason for adopting the ecological rather than the taxonomic arrangement of species. The objective of forest entomology to regulate insect numbers in such a manner that their activities do not cause economically important losses is continually kept in mind, and control procedures are fitted to current and future forest practice as closely as possible. This ecological and practical approach seems essential if the principles of forest entomology are to be understood and applied by foresters.

Experience has indicated a demand for information concerning contemporary work and workers in forest entomology. In order to meet this need, a section covering this subject is now included at the end of the historical review. Also a chapter on some indirect effects of forest insects, especially in connection with their influence in the dissemination of other insects and organisms that cause diseases of trees, has been added at the end of the book. Although our knowledge of these relationships is at present limited, there are indications that in the future important advances in this field may be expected. This chapter is intended to introduce the student to this important subject by presenting some of the more salient facts and by indicating ways in which these indirect effects may influence the forest.

These changes and additions have resulted in increasing the size of the book slightly, but it has still been kept within reasonable textbook length. In many instances new illustrations have been substituted for old ones, and others have been added to illustrate new sections. Most of these have not previously been published.

Although "Principles of Forest Entomology" is primarily intended to fill the need for a textbook in forest entomology, it is also hoped that its use will not be limited to the classroom. The principles set forth herein should be of interest not only to students and teachers of forest entomology but also to economic entomologists, ecologists, foresters, and many others engaged in growing or utilizing forest products.

No detailed consideration of the classification, structure, and metamorphosis of insects is included here, partly because it is felt that in the brief space available these subjects could not be covered adequately and partly because these subjects are thoroughly discussed in a number of easily available and excellent works that may be referred to for this information.

References to numerous species that have not been discussed in the text have been included in the bibliography for the convenience of those who may wish to refer to them. References to the bibliography are indicated in the text by the name of the author followed by the year of the publication referred to. The bibliography has been classified according to chapters and placed at the end of the book so as to simplify its use for general reference. No attempt has been made to cite references cover-

ing any subject completely, but, instead, selections have been made from easily accessible material that will serve as a starting point for a more extensive examination of literature.

The illustrations have been drawn from various sources. Some of them are photographs taken by the author, and many have never been used in previous publications. For permission to use certain illustrations, the author wishes to acknowledge his indebtedness to the Division of Entomology and Economic Zoology, University of Minnesota; the Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture; and The Entomological Branch, Canada Department of Agriculture; Mr. J. C. Evenden; Mr. A. A. Granovsky; and Mr. Leslie W. Orr. Mr. William Middleton, Dr. T. E. Snyder, and Mr. J. M. Miller were especially helpful in aiding in the selection of photographs from the files of the Bureau of Entomology.

During the preparation and revision of this work, valuable advice has been received from many entomologists and foresters. Encouragement and suggestions were received from members of the Division of Entomology and the Department of Animal Biology, University of Minnesota, especially Dr. W. A. Riley and Mr. A. G. Ruggles. Dr. R. N. Chapman examined certain sections and made many valuable suggestions concerning them; Dr. A. G. Boving very kindly examined the historical section; many others, from time to time, have offered suggestions, including Dr. J. J. Davis, Dr. F. C. Craighead, Dr. T. E. Snyder, and Professor Harry Smith. The author wishes to express his appreciation to all who have aided either directly or indirectly in connection with the preparation of this book.

Finally, the author wishes to acknowledge his obligation to his wife, Sybil Fleming Graham, and to express his appreciation of her valuable assistance in the preparation of this book for publication.

Samuel Alexander Graham.

School of Forestry and Conservation,
University of Michigan,
June, 1939.

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PRINCIPLES OF FOREST ENTOMOLOGY

CHAPTER I

INTRODUCTION

Forest entomology is that branch of the biological sciences which deals with insects in their relation to forests and forest products. The majority of species treated in this book have a direct effect either upon the trees themselves or upon the products derived from the trees. Some, however, have an indirect effect in that they are predaceous or parasitic and prey upon the tree pests. In addition to these two types there is, entering into the forest economy, a multitude of insects that are neither pests of trees nor parasitic or predatory enemies of those pests. Examples of these are insects that live upon the plants of the undergrowth, those that aid in the disintegration of waste wood in the forest, and those that feed upon the organic matter in the duff layer of forest soils. There can be no doubt that insects of this type play an important, if secondary, part in the forest. But they have received scant attention from entomologists, and, hence, little is known of their activities.

Importance of Forest Entomology in Forestry.—It has been said that forestry is 90 per cent protection. One may not accept this high percentage as a fair estimate of the importance of protection, but it must be admitted that, if our forests are not to be protected from the devastation of forest fire, and the ravages of insects and of fungous diseases, there will be little opportunity to practice forestry. Fire, fungi, and insects are the greatest agents of destruction in our forests. Any program of protection that ignores any one of this formidable triumvirate endangers our present and future timber supply and certainly invites disaster.

During every stage in the growth of wood, from the seed to the finished product, important insect problems are continually

presenting themselves. Even before the seeds are collected, they may be attacked and injured by certain insects that feed upon the seed of either coniferous or deciduous trees. These are, for the most part, members of the families Scolytidae (Ipidae), Curculionidae, or Chalcididae (Fig. 1). Deterioration of the seed, due to the activities of these insects, may continue during storage. In the nursery, the seedlings or transplants may be injured by such defoliators as climbing cutworms, or by root-eating insects

FIG. 1.—*Megastigmus spermatophilus*, one of the seed-eating chalcids, ovipositing in a douglas-fir cone. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

like white grubs and wireworms. Bark beetles, leaf or bud miners, plant lice, and scale insects all take their toll from the trees in the forest nursery and also from the advance growth of young trees growing under more natural conditions in the forest.

Trees in the sapling stage are sometimes attacked and severely injured by defoliators, phloem insects (Fig. 2), and sucking insects. The vigorous period between the sapling stage and commercial maturity is, as a rule, the stage most resistant to insect attack. Occasionally, even in this period, the trees may

succumb to the attack of defoliators or primary bark-beetles. With approaching maturity the vitality of the trees appears to be reduced, and they become increasingly susceptible to insect injury. Bark beetles that cannot kill vigorous young trees may breed successfully in the trees of the mature forest, and defoliators become much more dangerous than they were when the trees were in the full vigor of youth.

Later, when the trees die or are cut, they promptly become subject to the attack of the many kinds of wood-deteriorating insects. Bark beetles, ambrosia beetles, round-headed borers (Fig. 3), and flat-headed borers all attack and injure dying or recently killed trees and freshly cut wood. Not only do these insects injure the wood directly by their borings, but they are often responsible for the introduction of wood-staining and wood-

FIG. 2.

FIG. 3.

FIG. 2.—A white-pine sapling injured by the white-pine weevil. The top of the main stem has been killed. This kind of injury frequently produces a crooked tree.

FIG. 3.—*Monochamus obtusus* adults on a ponderosa pine log from which they have emerged. Note the circular emergence holes characteristic of this and other round-headed borers. These insects are injurious to freshly cut or recently killed timber. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

rotting organisms. As the wood seasons or decays, it becomes subject to the attack of numerous other insects.

With such a multiplicity of insect species attacking trees and wood products, it is difficult, indeed, for a forester to find any line of forestry work in which he is not faced by some insect problem. Even the lumber salesman may be called upon to

FIG. 4.—The work of powder-post beetles in finished lumber. (*University of Minnesota.*)

pacify a customer who finds powder-post beetles (Fig. 4) emerging from a newly laid hardwood floor. Also, in lumber manufacturing, in the pulp and paper industry, in forest by-product industries, and in the more technical phases of forestry work, entomological problems are forever intruding.

In the past, in spite of the tremendous losses caused by insects of forests and forest products, entomology has often been looked

upon in forestry as something to be ignored whenever possible. This was due, in part at least, to the feeling among foresters and lumbermen that insects in the forest could not be controlled, and therefore they were given scant attention. But this point of view is rapidly changing, and forest entomology is now properly considered to be an integral and important part of forest protection. Forest entomological problems can no longer be disregarded. They must be faced squarely and solved together with our problems in silviculture, management, and utilization.

It is important, therefore, that every forester should be able to recognize evidences of possibly dangerous insect activities and should know enough about insect pests and their control to approach problems intelligently. He should know how and where to obtain information about insects and should be able to apply the necessary remedies intelligently. A person totally ignorant of insects and their ways cannot hope to get the best results, any more than a poorly trained physician can hope to give as good service as one who is well acquainted with the disease he is called upon to cure.

Losses Due to Forest Insects.—It is undoubtedly true that in North America more wood has been destroyed by insects, fungi, and fire than has ever been cut and used. Of the various wood destroyers, insects are by no means the least important.

Accurate estimates of losses due to forest insects are very difficult to obtain. In only a few instances have systematic loss records been made year after year, and even these are relatively

Losses Due to Bark Beetles in California

Year	B.M. Destroyed, Millions Feet
1925	750
1926	1,000
1927	1,200
1928	900
1929	600
1930	500
1931	1,250
1932	1,500
1933	800
1934	750
1935	700
1936	500
1937 (Incomplete records)	300

fragmentary. The records of losses in the West due to bark beetles are perhaps the best available. They are based on records made annually on a considerable series of sample areas and assume that similar damage occurs on other similar areas.

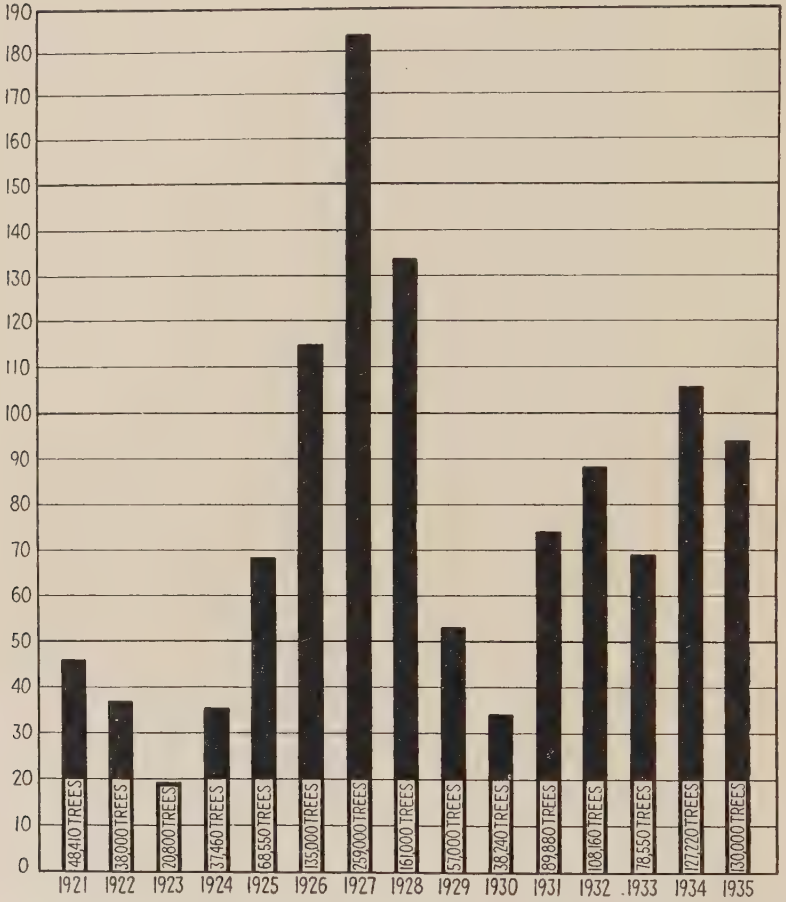


FIG. 5.—The volume of ponderosa pine killed annually from 1921 to 1935 by bark beetles on an area in Northern California. Note the number of trees dying from year to year, as indicated by figures. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

In 1928 it was estimated by the Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture, that the average annual loss due to the attack of bark beetles in western

pine and spruce was 5,000,000,000 feet b.m. The average loss in California alone has been estimated at 500,000,000 feet b.m. annually. Since 1928 in that state, the loss estimated on the basis of plot surveys (Fig. 5) has exceeded the average each year except 1930, 1936 and 1937, which were years of relatively light injury. The tabulation on page 5 indicates how these losses have varied from year to year (Salman, 1937).

These records indicate how damage caused by insects may vary from year to year. Even greater fluctuations may occur in

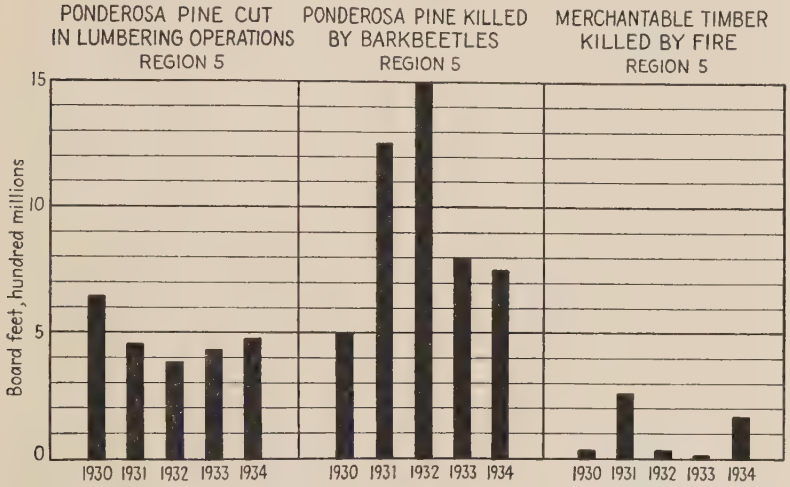

PONDEROSA PINE CUT IN LUMBERING OPERATIONS REGION 5
PONDEROSA PINE KILLED BY BARKBEETLES REGION 5
MERCHANTABLE TIMBER KILLED BY FIRE REGION 5
Board feet, hundred millions
15
10
5
0
1930 1931 1932 1933 1934
1930 1931 1932 1933 1934
1930 1931 1932 1933 1934

FIG. 6.—Comparison of forest depletion caused by fire, fungi, and insects in Region 5, U. S. Forest Service. The relatively low fire damage indicates the effectiveness of fire suppression and prevention. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

longer periods of time. It seems likely that the losses during the last two decades on the West Coast have been higher than normal, owing in part to the large bodies of overmature timber in the forest, and in part to precipitation deficiency, which seems to be correlated with injury by the western pine-beetle (Keen, 1937). Another period when more favorable precipitation prevails may likely see a marked reduction of the present rate of loss due to bark beetles.

On the basis of recent survey records, Beal reports the annual loss resulting from the attack of *Dendroctonus ponderosae* in the central Rocky Mountain Region as follows:

State	Feet b.m. destroyed	1937 cut of pine, feet b.m.
Colorado	15,000,000	51,907,000
Wyoming	69,150,000	35,706,000
Utah	7,500,000	5,730,000

In addition to the losses due to bark beetles in the West, some outbreaks of other insects have been of such a character that the approximate losses can be estimated with reasonable accuracy. A few of these are as follows:

1. Spruce budworm in Quebec, 1910 to 1920, 200,000,000 cords of balsam fir.

2. Spruce budworm in Minnesota, 1913 to 1923, 20,000,000 cords of balsam fir.

3. Spruce budworm in New England, 1910 to 1920, 15,000,000 cords of balsam fir.

4. Spruce budworm total, 1910 to 1925, 235,000,000 cords of balsam fir[1] (Fig. 7).

5. Larch sawfly in Minnesota, 1910 to 1926, 1,000,000,000 feet b.m. of tamarack, and in the entire range of eastern larch at least twenty times the preceding figure was destroyed in the same period.

Between 1926 and 1938, the injury caused by the larch sawfly has been practically negligible, and it seems unlikely that it will again become very serious until another crop of tamarack has grown up to replace the trees killed. This condition will probably not develop before 1950 or possibly 1960, after which another general outbreak may be expected.

Likewise with the spruce budworm, the period between outbreaks depends upon the length of time required to replace the trees destroyed and bring the forest to a condition favorable for an outbreak. Thus the approximate annual loss will be the loss sustained during an outbreak divided by the number of years between the beginnings of outbreaks. On this basis the annual loss caused by the spruce budworm to eastern balsam fir, assuming a period of 50 years between outbreaks, is in the neighborhood

[1] This does not include several comparatively recent outbreaks in Canada and the United States concerning which no data are available.

of 4,700,000 cords, and that caused by the larch sawfly 400,000,000 feet b.m.

Even the foregoing estimates, based as they are upon field observations, cannot be looked upon as being very exact

FIG. 7.—Diagramatic cross sections of two forest areas, illustrating the effect of a spruce-budworm outbreak upon forests of different compositions. Balsam fir is represented by a narrow, unshaded cone, pine by a broad cone, other conifers by a shaded cone, spruce by the figure with drooping branches, and hardwoods by an oval. The upper line of trees represents the original condition before the outbreak, the lower, the condition after the outbreak. The relative size of the trees is indicated by the height of the figures. *A*, represents a mixed stand composed mostly of balsam fir and hardwoods. *B* represents a stand where balsam fir was originally the predominating species. Note that the injury to the forest is much more severe where balsam fir is most abundant.

They must, of necessity, rest on a comparatively small number of accurate measurements and a great deal of general observation, with the result that the probable error is high. It must also be kept in mind that a considerable portion of the timber killed by both the spruce budworm and the larch sawfly was located in

areas that were, and still are, inaccessible for logging. In many instances, it is probable that by the time some of these forests will be needed to supply our demands for this kind of timber a new crop of merchantable trees will have replaced those killed (Fig. 8). Thus, although the destruction of timber has been almost beyond human conception, the actual economic loss is somewhat less than it might at first appear to be. The destruc-

FIG. 8.—A tamarack forest killed by the larch sawfly. Spruce and young tamarack are replacing the trees killed.

tion of this timber, therefore, was not nearly so serious a matter as will be similar outbreaks in the future.

The losses resulting from such outbreaks of insects as those cited above represent only a part of the total damage for which forest insects are responsible. To these losses must be added the less conspicuous but none the less real damage caused by insects present in normal numbers. The amount of this loss has been estimated in various ways. One of these is to assume a loss of 10 per cent of the total annual cut. On this basis the average annual loss in the United States for the years 1925–1929

amounted to 5,913,383,900 feet b.m. Whether or not such an estimate is justified by the facts is obviously open to question.

The destruction of manufactured wood-products by insects certainly amounts to a very high total, but no definite data are available at present on which to base an estimate. Termites,

FIG. 9.—Timbers in the White House, Washington, D. C., damaged by wood-boring insects (*Hexarthrum ulkei*). This injury necessitated the replacement of the timbers at considerable expense. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

especially in tropical and subtropical regions, are particularly injurious to unprotected wooden structures. Even in the temperate regions of this country, particularly along the Atlantic and Pacific coasts, termites are sufficiently numerous and injurious to justify special building regulations to avoid injury to wooden structures by these insects. Other insects, such as the powder-post beetles and the pole borer, attack and destroy seasoned wood and finished products, but the data available

are insufficient to form the bases for satisfactory damage estimates (Figs. 9 and 10).

Incomplete and unsatisfactory as our statistics may be, they are, at least, sufficient to indicate that insects are an important economic factor in our forest industry and should receive an important place in our plans for the protection of our forests and forest products.

Scope and Subdivisions of Forest Entomology.—The scope of forest entomology is wider than may at first appear to be the case.

FIG. 10.—One of the Internal Revenue buildings in Washington, D. C., injured by termites to such an extent as to necessitate the replacement of the supporting timbers. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

It includes a great variety of materials leading to the better understanding of the biological phenomena of forest life. The ultimate aim of forest entomology is to make possible the regulation, in the interest of man, of insect activities in forest and forest products. In the control of forest insects, directly protective methods can seldom be applied, because of the excessive cost of such operations. As a rule, one is compelled to resort to preventive rather than to curative methods. This preventive entomology calls for a much more profound knowledge of both the insects and the forest environment than would be required if one could depend largely upon direct control. One of the first

requisites for forest insect work, therefore, is a sound basic knowledge of silvics and silviculture. Not until one knows his trees is he in a position to apply his entomological knowledge to them.

On the other hand, one must know his insects. To know an insect one must not only be able to recognize the genus and species to which it belongs, but he must also understand its functions, its reactions to its environment, and its physical limitations. Thus, all the major divisions of the science of entomology are needed in the solution of forest entomological problems. Taxonomy is needed in classifying insects and to indicate their relationship and origin. It not only aids the forester by giving names, but also, whenever a new forest entomological problem presents itself, may actually furnish the key to satisfactory control measures. For closely related insects can often be controlled by similar means, and the service of taxonomy in showing relationships of new to old pests may often prove invaluable. Studies in morphology, histology, and physiology of forest insects lead to a more complete knowledge of the insects studied and aid directly or indirectly in the solution of forest entomological problems. Chemical entomology, which includes spraying, dusting, and fumigating for the control of insect pests, has its place in the control of certain tree insects. Ecological studies, including life-history investigations, the effect of climatic and other environmental factors upon forest insects, and the interrelation of parasites and predatory species with their hosts, are all of fundamental importance in forest entomology.

Obviously, no forest entomologist can be expected to have the detailed knowledge of taxonomy that is expected of a specialist in taxonomy and at the same time be a specialist in morphology, histology, physiology, ecology, and chemical entomology. The field is too large to permit of such a wide scope of endeavor. On the other hand, he is expected to have a general knowledge of each of these fields and to have a detailed knowledge of some of them. At the present time, forest entomologists in the United States and Canada are centering their attention for the most part upon either taxonomy or ecology, or both; in Europe, however, at least some of the workers in forest entomology are attacking problems of a morphological, histological, or physiological nature. It is probable that the future may see the

development of specialists within the field of forest entomology just as we now have specialists in other fields of entomology. If such specialization does come to pass, let us hope that the workers will avoid the danger of overspecialization and will continue to maintain their grasp of the general field, and thus keep a proper perspective of forest entomology as a whole.

Forest Entomological Literature.—Every student must rely on the writings of others for a foundation of information in any

FIG. 11.—Injury by a pitch-blister moth on pine. *Petrova sp.* This injury seldom kills trees but may cause breakage of the leader and side branches at a whorl.

given line. The ability to locate all available literature on any subject and to use that literature efficiently is essential for best results. The library is one of the most important tools. In the field of forest entomology there is particular need for training in the ways and means of locating information, because the writings in this field are so scattered that they are sometimes difficult to find and may easily be overlooked.

Fortunately for the student of forest insects, American economic entomology is unusually well provided with a series of

indexed bibliographies published by the United States Department of Agriculture and by a series of indexes published by the American Association of Economic Entomologists. Volumes I to V, inclusive, of the indexed bibliography entitled, "Bibliography of the More Important Contributions to American Economic Entomology," were compiled by Samuel Henshaw. The first three volumes were devoted to the writings of B. D. Walsh and C. V. Riley, two men who were perhaps the most prolific writers that entomology has ever known. Volumes IV and V cover the writings of other authors up to 1888. Volumes VI to VIII, inclusive, of this series were compiled by Nathan Banks and cover the period from 1888 to 1905. The series was then discontinued by the Department of Agriculture. The work was later taken up by the American Association of Economic Entomologists, and the index portion continued. The first volume of this index was compiled by Banks and covers the years 1905 to 1914, inclusive. Since then four more volumes have appeared, compiled by Mabel Colcord. Each of these covers a period of 5 years.

These bibliographies and indexes provide a ready means of access to most of the important economic entomological literature of the United States and Canada, but they do not help where other literature is concerned. For this, one must go to other works, the most important of which is probably the *Zoological Record*. This record has been published annually since 1864 by the Zoological Society of London, and aims to include all publications dealing with animals. A large part of each volume is devoted to entomological literature. Periodical index numbers are published. For information previous to 1864 one may go to the "Index Literaturae Entomologicae," compiled by Hagen, Horn, and Schenkling.

Owing to the fact that much forest entomological information has been published in forestry journals, trade journals, and other publications, not ordinarily examined in the compilation of the bibliographical aids just mentioned, the forest entomologist must not neglect forestry literature or he may miss important contributions. This is particularly true of European literature. No indexes in English of forestry literature comparable to those of entomological literature have ever been published. This lack adds to the difficulty of bibliographical work. The *Journal of*

Forestry and its predecessor, the *Forestry Quarterly*, published monthly lists of literature beginning in 1902, and thus provided a readily accessible reference to many forest entomological articles not included in entomological bibliographies and indexes, but in recent years these lists have been discontinued. The older volumes are still a valuable bibliographic aid.

The indexes and records mentioned above aid the student in his search into the past, but this is only a part of his problem. Often several years may pass between the date of publication of an article, and the publication of an index referring thereto. This gap must be bridged, which is no light task when one considers the scores of periodicals, bulletins, circulars, and books coming from the press each month that may contain forest entomological information. Even though each worker had access to every article in the mass of literature, he could scarcely be expected to take the time to examine all of them. As a time saver and an aid in keeping in touch with recent progress, the reviewing and abstracting periodicals are a great aid. These publications are usually only a few months behind the publication of original papers.

One of the most important reviewing organs for the entomologist is the *Review of Applied Entomology*, published in London by the Imperial Bureau of Entomology. This publication appears monthly and aims to review every article published in the field of economic entomology. It is world wide in its scope and misses very few publications of importance. In the United States, the *Experiment Station Record*, published by the U. S. Department of Agriculture, covers a large part of the American literature. Since 1928 *Forstliche Rundschau; der zeitschrift für Weltforstwirtschaft* has covered the forestry literature of the world, including forest entomological titles. This publication appears quarterly.

Biological Abstracts, a publication starting with January, 1926, has superseded most of the older abstracting agencies, because it covers the entire field of biology. By bringing together world-wide biological literature in this way the problem of the individual worker in keeping abreast of the times is greatly simplified.

Convenient and useful as they may be in helping workers in the various fields to keep abreast with scientific progress, there lies a danger in the use of these abstracting periodicals: the danger that one may neglect to read original articles. It must

be remembered that an abstract does not take the place of the original but serves only to indicate whether or not the original is of sufficient importance to be read. The student of entomology must be familiar with all the original sources that apply to the work at hand.

Some of the sources in which one ordinarily expects to find American and Canadian forest entomological work published may be listed as follows:

1. U. S. Department of Agriculture:
   - Department bulletins and circulars.
   - Bureau of Entomology and Plant Quarantine bulletins and circulars.
   - Farmers' bulletins.
   - Yearbooks and reports.
2. State Publications:
   - Experiment station bulletins, circulars, and reports.
   - University bulletins and memoirs.
   - State entomologist publications.
3. Bulletins and Circulars of the Entomological Branch, Canada.
4. Periodicals:
   - *Journal of Economic Entomology.*
   - *Journal of Agricultural Research.*
   - *Journal of Forestry.* (*Forestry Quarterly* and *Proceedings of the Society of American Foresters.*)
   - *Canadian Entomologist.*
   - *Canadian Lumberman.*
   - *American Lumberman.*
   - *The Timberman.*
   - *Proceedings of the Washington Entomological Society.*
   - *Proceedings of the Entomological Society of Ontario.*
   - *Proceedings of the Entomological Society of Nova Scotia.*
   - *Proceedings of the Entomological Society of British Columbia.*

References to various of these pamphlet and periodical publications will be found in the bibliography.

In England, a considerable proportion of the forest entomological work is conducted by the Forestry Commission and is reported in its publications. Other articles appear from time to time in the *Journal of Ecology* and other periodicals. Still other articles on entomology are published in the *Indian Forester*, and official publications of the Indian Government, and also in the official publications of the respective governments of Australia and South Africa. In addition to publications printed in English, there are many periodicals in foreign languages,

particularly German. Of these one of the most outstanding at the present time is the *Zeitschift für angewandte Entomologie* edited by Escherich. Almost all the European forestry and entomological publications print occasional papers on forest insects.

Although the major portion of European forest entomological literature appears in the form of pamphlets and short articles, there are a number of important books on the subject. In America, however, forest entomological books are very few. In fact, there is no general comprehensive work comparable with some of those that may be cited from European countries. About the only American books that deal with forest insects are:

Packard, 1890, "Insects Injurious to Forest and Shade Trees." Fifth Report of the Entomological Commission, U. S. Dept. Agr.
Felt, 1905, "Insects Affecting Park and Woodland Trees." *Mem.* 8, New York State Museum.
Felt, 1924, "Manual of Tree and Shrub Insects."
Essig, 1929, "Insects of Western North America."
Chamberlin, 1931, "An Introduction to Forest Entomology."
Felt and Rankin, 1932, "Insects and Diseases of Ornamental Trees and Shrubs."
Herrick, 1935, "Insect Enemies of Shade Trees."
Doane, Van Dyke, Chamberlin, and Burke, 1937, "Forest Insects."

One of the best manuals of general entomology is:

Comstock, 1936, "An Introduction to Entomology."

Some of the outstanding English and European texts are:

Gillanders, 1908, "Forest Entomology."
Escherich, 1914, 1923, and 1931, "Die Forstinsekten Mitteleuropas" (A revision of Judeich and Nitsche's "Lehrbuch der Mitteleuropaischen Forstinsektenkunde").
Trägårdh, 1914, "Sveriges Skogs Insekter."
Cecconi, 1922, "Manuale di Entomologia Forestale."
Nüsslin-Rhumbler, 1922, "Forstinsektenkunde."
Barbey, 1925, "Traité D'Entomologie Forestière."
Chrystal, 1937, "Insects of British Woodlands."

Because forest entomological literature is so widely scattered is so many different publications, it is obvious that no local library can have on its shelves copies of all the entomological publications that one may wish to examine. Even in some of our best entomological libraries, it is often impossible to find

every article that may be of interest. Fortunately, however, most of the local libraries have the privilege of borrowing from other libraries, or, if the publications themselves cannot be borrowed, photostat copies of parts of articles or books can usually be obtained; consequently, if one has a definite reference, it is usually possible to see a certain publication even though the facilities of the local library are rather limited. The first and most important thing that one needs when one begins to look up the literature on any subject is to have at hand adequate bibliographical aids in the form of indexes and abstracting organs, such as have been mentioned above. With these at one's command, one can search through literature effectively; without them, one is helpless. One should see, therefore, that the local libraries are equipped with at least these very necessary tools.

CHAPTER II

HISTORICAL REVIEW

The science of forest entomology, like the science of forestry of which it is a part, is very young. It had its beginning during the first part of the nineteenth century.

DEVELOPMENT IN EUROPE

Inasmuch as Germany was the first country to develop forestry, it is natural that in that country forest entomology should have had its inception. As the value of trees became more and more appreciated and methods of silvicultural practice were developed, the necessity of protecting the trees from the ravages of insects became increasingly important.

The Pre-Ratzeburg Period.—The outbreak of a forest pest was something with which the early foresters were unable to cope, and so they were forced to call on others for help. They appealed to the zoologists. As a result of these early appeals, a number of publications appeared that dealt with various individual forest insect problems. For instance, one finds such treatises as that of Gmelin, "Abhandlung über die Wurmtrocknis," published in 1773, and that of Hennert, "Uber die Raupenfrass und Windbruch," published in 1798.

The purpose behind most of these early studies of forest insects was the development of methods by which a certain pest or the pests of a certain tree might be controlled. It is true that this end was seldom accomplished, and that the chief contribution of these studies to science was either taxonomic or biologic in character. Sometimes, however, effective measures were suggested and applied. For instance, Linnaeus is said to have recommended that freshly cut logs be floated in water to prevent injury by borers—a very effective method that is in use today.

Previous to 1800, forest entomology, as such, did not exist. There were no specialists in this subject, and the studies of tree

insects were conducted by men whose primary interest was in other lines of work. The first attempt to gather together all available information concerning forest insects was that of Beckstein and Scharfenberg who published, in 1804 and 1805, two volumes entitled, "Vollständige Naturgeschichte der für den Wald schädlichen und nützlichen Forstinsekten." This was a very pretentious compendium of forest insect information, and for a period of 30 years was the only general work available on the subject.

The Period of Ratzeburg.—Then there appeared a monumental work which even today has never been surpassed in excellence and scope. This was Ratzeburg's "Die Forstinsekten." Ratzeburg was the first man to devote all his energies to forest entomology, and he has frequently been called the father of forest entomology. He lived in an age when specialization was the exception rather than the rule. Even he attempted at first to cover forest pathology as well as forest entomology, but he soon found that these two subjects were too extensive to be handled effectively by any one man. His later work, therefore, was confined to the field of entomology.

The first volume of "Die Forstinsekten" appeared in 1837, the second in 1840, and the third in 1844. He also published a handbook, "Die Walverderber und ihr Feinde," that summarized in more condensed form the material contained in "Die Forstinsekten." The demand for this handbook was so great that by 1869 it appeared in its sixth edition. After Ratzeburg's death, in 1871, this book continued to appear in new editions edited by his successors. Judeich and Nitsche published a book which purported to be a revision of this work of Ratzeburg's (1885) in two volumes under the title "Lehrbuch der mittleuropaischen Forstinsektenkunde." Still more recently, Escherich has published a new edition, which is a masterpiece of its kind, under the title "Die Forstinsekten Mittleuropas." Escherich has added much new material and has rewritten the older portion of the book, thus making a thoroughly modern presentation of the subject. Ratzeburg continued to publish during his long and productive life. One of his best-known works is his "Ichneumoniden der Forstinsekten," published in three parts in 1844, 1848, and 1852. Ratzeburg dominated the period during which he lived. But although he stood head and shoulders above his

contemporaries, there were other workers who made very valuable contributions to the science of forest entomology. Among them we find Kollar, Hartig, and Nordlinger in Germany, and Perris in France. The most important contribution of Kollar is a "Treatise on Insects Injurious to Gardens, Forests and Farms." It has been translated from the German. Perris is credited with the first experimental studies in forest entomology. He cut trees at different seasons and studied the life history and habits of the various insects that attacked them. His greatest contribution was the "Histoire des Insectes du Pin Maritime," which appeared in ten parts between 1851 and 1870 in the Annals of the Entomological Society of France.

The Period of Eichhoff.—Up to the time of Ratzeburg's death, the chief emphasis in forest entomology was placed on the biological studies. These investigations were often in the nature of general natural-history studies and were usually not based upon controlled experimental evidence. The work of Eichhoff ushered in a new era, which made of forest entomology a more exact science than it had previously been. By combining careful biological experiments and detailed systematic studies, he cleared up many misconceived notions concerning the biology of bark beetles and set up a model for other investigators to follow. His outstanding contribution, entitled "Europaischen Borkenkäfer," was published in 1881.

During the later part of the nineteenth century there were, particularly in Germany, many workers who devoted a part or all of their time to the study of forest insects. Among them was Altum, at Eberswalde, who did much by his work to stimulate investigation and discussion as a result of the theories and hypotheses that he proposed. Nitsche, at the Forstakademie in Tharand, and Henschel, at the Agricultural High School at Wien, were both outstanding teachers and investigators.

The Modern Period of Europe.—From the very beginning until the end of the nineteenth century, European forest entomologists looked to Germany for leadership. This was the natural result of the tremendous amount of valuable pioneering work on forest insects produced by the entomologists of that country. Since the beginning of the twentieth century a decided change has been taking place until now, in the modern period, leaders in forest entomology, instead of being centered in a single

country, are to be found throughout those parts of the old world where forests are economically important. Germany still has her great men in forest entomology who are contributing much to the science; Escherich, Rhumbler, and Prell are some of these. But they no longer stand alone. Trägårdh in Sweden, Saalas in Finland, and Munro, Fisher, and Chrystal in England must all be regarded as leaders in their field.

In Europe, the science of forest entomology has, in general, passed through several more or less definite periods. The first was the natural-history period that was characterized and dominated by the work of Ratzeburg. The second was the period of great taxonomic activity supplemented by experimental life-history studies. Eichhoff characterizes this stage which was really the connecting link between the first period and the third. In the third, or modern, period the great emphasis is placed on experimental biology. One of the outstanding figures in the early part of this period was Nüsslin. He has been followed by a host of other workers, among them Hennings who was the first to study bark bettles under controlled temperature and humidity. Unfortunately for forest entomology, his work was cut short by his untimely death.

DEVELOPMENT IN AMERICA

During Ratzeburg's period of domination in Europe, an interest in tree insects was developing in America.

The Natural-history Period in America.—The earlier contributions in America, like those in Europe, dealt largely with forest-insect biology from the natural-history viewpoint. These early writings are both useful and interesting to us today, but unfortunately they are so scattered in various publications that they are sometimes difficult to obtain. However, most of this material is referred to in the indexes already discussed. Many articles on tree insects are included in Harris's "Treatise on Some of the Insects Injurious to Vegetation" (1886) and in Fitch's reports on "Noxious, Beneficial and Other Insects of the State of New York" (1856 to 1870). The reports and articles of Walsh, Riley, Lintner, Comstock, and Forbes also contain much information concerning forest insects.

But it was not until 1890 that the first compendium on American forest insects was published. At that time Packard brought

together all the available material in the fifth report of the Entomological Commission of the U. S. Department of Agriculture entitled, "Insects Injurious to Forest and Shade Trees." This report contains a mass of valuable information concerning tree insects and is well illustrated by numerous plates and figures. Packard included verbatim many of the important articles by other authors which are not, as a rule, easily accessible, and this adds materially to the value of his book for reference. For years, Packard's report was the only comprehensive work on American forest insects. Then, in 1905, was published *Memoir* 8 of the New York State Museum, by Felt, entitled "Insects Affecting Park and Woodland Trees." This added some new information to that included in Packard's report, but its chief value was in its remarkably fine colored illustrations.

The Taxonomic-biological Period.—Then followed a period when taxonomic-biological studies predominated in forest entomological work. This period was similar in character to the Eichhoff period in Europe, the influence of which was evident upon American work of the early part of the present century. Hopkins in his bark-beetle studies has added much to our knowledge of that group of insects both biologically and taxonomically. He was able by his work, like Eichhoff, to dispel many incorrect views that had previously been held concerning both the bark beetles and the bark weevils.

Much of the work of both Swaine and Blackman belongs in the taxonomic-biological category, and some of the earlier work of Craighead was along similar lines, but later all three of these men worked along the lines of experimental biology.

In recent years, Swaine has shifted his activities from forest entomology, becoming director of research, now in charge of Science Service, in the Department of Agriculture of Canada. He has been succeeded in the Division of Forest Insects by J. J. de Gryse.

Blackman is now devoting his energies entirely to taxonomic studies, and Craighead's administrative duties as chief of the Division of Forest Insect Investigations, Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture, have come to take more and more time from his research. The places of these men in the field of research are being filled by younger men, some of whom will be mentioned in a following section.

During the early periods in America the emphasis was placed on shade-tree insects. Virgin forests were still supplying an abundance of wood products, and the practice of forestry was practically unknown, because it was unnecessary. The few methods of forest-insect control that were mentioned in the publications of that time were for the most part borrowed from continental Europe. This situation has continued until very recently. Even today tree insects are receiving much more attention as shade-tree pests than they are as enemies of the forest. But a rapid change in point of emphasis is now taking place.

The Modern Period in America.—In Europe, the emphasis, since the earliest development of the science, has been placed on insects of the forest. This has been the result of economic conditions, characteristic of densely populated communities, where a scarcity of wood has made the practice of forestry a necessity. The forest entomological investigations, moreover, have been centered in the forest schools as an integral part of the forestry work. In America, on the other hand, the work on tree insects has, until recently, been conducted in a large measure by entomologists whose interests and training were in no way connected with forests or forestry. As a result, the insects have been studied primarily for their own sake and their relationship to the forest has consequently often been of subsidiary importance.

The modern viewpoint of forest entomology is quite different, however. As forestry has developed in America there has been an ever-increasing need for information concerning the influence of forest insects upon the forest. Where in the past there were almost no men spending their entire time upon forest-insect problems, there are now many capable men employed in this work. These men are interested both in the insects themselves and in the forest, but their primary interest is in the influence of insects upon the forest.

This point of view has resulted during recent years in the application of experimental biological methods to forest entomological problems. Purely observational methods of study have been largely abandoned, and taxonomy is no longer thought to be an end in itself but merely one of the useful tools of the profession. Life-history studies are likewise regarded as means

to an end rather than ends in themselves. The interrelations of insects with one another and with the various other elements of the forest environment are coming to be regarded as more and more important.

Thus the development of forest entomology in America has passed through stages that are more or less comparable to the development of this branch of science in Europe. The first or natural-history period was contemporaneous with a similar period in Europe. So also was the taxonomic-biological period contemporaneous with similar efforts in the Old World. The application of the methods of experimental biology, likewise, appeared in Europe and America about the same time. These methods have led to the recent rapid development in the fields of ecology, physiology, genetics, and biometry. Forest entomology, like the other biological sciences, is now being built up rapidly on the basis of experimental work.

Contemporary Work and Workers in America.—Students frequently ask where and by whom is forest entomological work being conducted. Because this information is not readily obtainable from current literature, a brief statement is introduced here, recognizing, of course, that the picture as it exists at present may soon change.

By far the greater part of the forest entomological work in the United States is carried on by the Bureau of Entomology and Plant Quarantine of the U. S. Department of Agriculture. As previously stated, Dr. F. C. Craighead is chief of the Division of Forest Insect Investigations, a position that he has occupied since 1921, when Dr. A. D. Hopkins, the former chief, retired.

The Division of Forest Insect Investigations, like most of the other divisions of the Bureau of Entomology and Plant Quarantine, except the purely regulatory units, serves the double function of service and research. Service consists of providing the U. S. Forest Service, the National Park Service, the Indian Service, the various state services, and private timberland owners with the latest information concerning forest insects. It also provides specific advice to all other government agencies as to the necessity of conducting control operations in specific cases, the approximate cost of such operations, the methods to be followed, and the technical supervision of the work. The research activities consist primarily of field and laboratory

investigations, the purpose of which is to obtain information that can be applied to practical forest entomological problems.

The actual investigations and most of the services are conducted or made available at field laboratories located in the various forest regions. Space will not permit a full discussion of the personnel and detailed research programs of each of the nine forest-insect laboratories, but each deserves brief mention.

The laboratory serving the Northeastern states is located at New Haven, Conn. This station has been concerned chiefly with investigations of insects injurious to second-growth timber. One of these that has received special attention is the white-pine weevil, an insect that is very injurious to young eastern white pine. At present special attention is being given to the study of parasites of forest insects. Much of this work was formerly conducted at the famous Gypsy Moth Laboratory that was located at Melrose Highlands, Mass. This laboratory has now been abandoned. Another laboratory that serves the Eastern states is located at Morristown, N. J. This laboratory is at present primarily concerned with investigation of the Dutch elm-disease but other shade-tree problems are also being investigated there.

The Southeast is served by a laboratory located at Asheville, N. C., and is in charge of B. H. Wilford. At this laboratory, Craighead and his associates determined the important relationship existing between the southern pine-beetle and the fungi that cause the blue staining of wood. They demonstrated that the fungus hastens the death of the trees attacked by the beetles by blocking the conductive tissues. Moreover, important studies in tree medication have been and still are in progress at this laboratory. Among the numerous workers who have contributed much to the success of the work at Asheville is R. A. St. George, who is now stationed in Washington, D. C.

The Southern states are served by the New Orleans, La., laboratory in charge of T. E. Snyder. Dr. Snyder is an outstanding authority on termites and their control. Therefore much of the work at this laboratory has been concerned with wood-destroying insects.

The laboratory located at Milwaukee, Wis., serves the Lake states. It was formerly located at the University of Minnesota and later at the University of Michigan in cooperation with these

institutions. H. J. MacAloney is in charge of this station, having recently been transferred from the New Haven laboratory to succeed L. W. Orr, who was moved to the Washington office late in 1937. The work of this laboratory has been chiefly concerned with defoliating insects. Since 1933 much attention has been devoted to the study of root-eating scarabaeid beetles (white grubs) that injure coniferous trees.

A temporary laboratory in Columbus, Ohio, in charge of R. C. Hall has recently been discontinued, and Dr. Hall has been transferred to the Berkeley, Calif., laboratory. The work of the Columbus laboratory was concerned chiefly with the study of the locust borer. These investigations have contributed much to our knowledge of this insect, which has been the chief cause of black locust plantation failures. The study of the locust borer promised to lead to its control through the development of better methods of handling black locust plantations than those in current use. It is to be hoped that these studies will not be too seriously interrupted by the discontinuance of the Columbus laboratory.

A laboratory at Fort Collins, Col., in charge of J. A. Beal, covers the forest-insect problems of the Southern and Central Mountains and the Great Plains. The workers at this laboratory have been especially concerned with insect troubles that have arisen in the plantations in the so-called Shelter Belt Zone, but they have also studied dendroctonus beetle and other insect problems.

Until recently, L. G. Baumhofer was located at this laboratory with Dr. Beal but he has been transferred to the Washington office. One of Baumhofer's most important pieces of work has been his studies of the pine tipmoth in the Nebraska National Forest.

One of the oldest forest-insect field laboratories of the Bureau of Entomology and Plant Quarantine is located at Coeur d'Alene, Idaho, and is in charge of J. C. Evenden. The area covered by this station includes the Northern Rocky Mountain Region, Montana, and a part of North Dakota. The work has been concerned especially with studies of the mountain-pine beetle in western white pine and lodgepole pine. Associated with Evenden at the Couer d'Alene laboratory are a number of workers, among whom are W. D. Bedard, who is engaged in

ecological studies of the mountain-pine beetle, and A. L. Gibson, who is studying various aspects of bark-beetle control.

The Pacific Northwest is served by a forest-insect laboratory located at Portland, Ore. It is in charge of F. P. Keen. This station is an outgrowth of work started in Oregon and Washington by the Berkeley, Calif., laboratory, with which Keen was formerly associated, and is especially concerned with investigations of the western pine-beetle in ponderosa pine and the mountain-pine beetle in sugar pine and lodgepole pine. One of the outstanding contributions is Keen's work on tree susceptibility including his studies of the relation between weather fluctuations and bark-beetle outbreaks in east-side type ponderosa pine. A very interesting series of investigations at this station, being conducted by R. L. Furniss, is concerned with the rate of deterioration of fire-killed timber.

The oldest forest-insect field station in the West is the Berkely, Calif., laboratory. This station is in charge of J. M. Miller. Numerous important insects have been the subject of investigation, including the lodgepole pine needle-miner, (Patterson, 1921), the fir engraver beetle (Struble, 1937), and various other insects. Since about 1920, however, investigations have been concentrated on dendroctonus beetles, especially the western pine-beetle, because of the tremendous losses caused in mature stands of timber by these beetles.

Studies of the composition of insect populations in dying trees, which have been conducted for years by various members of the staff, but which have been recently stimulated by the work of K. A. Salman, promise to lead to a better understanding of the relative importance of various insects as tree killers. Another aspect of the work at the Berkeley laboratory that promises to give us a better understanding of bark beetles and the importance of their natural enemies is the series of parasite and predator studies in which George R. Struble is now engaged.

All these field stations of the Bureau of Entomology and Plant Quarantine cooperate with other governmental agencies like the U. S. Forest Service, the National Park Service, and the Bureau of Plant Industry. Some of them are closely associated with universities and are conducting projects cooperatively with these institutions. This is true of the Berkeley station, which is located at the University of California, and the Lake states

station, which is conducting considerable research in cooperation with the universities of Michigan and Minnesota.

Outside the Bureau of Entomology and Plant Quarantine, organized programs of forest entomological research are rare. Most of the projects are more or less sporadic in nature, except for studies of shade-tree pests, which we shall not consider here. Only a few institutions have organized research programs.

At the University of California, the forest-insect studies, except for the cooperative projects with the Bureau of Entomology and Plant Quarantine, consist primarily of taxonomic and biological investigations by E. C. Van Dyke and his students. At Oregon State College, much of the work of W. J. Chamberlin has been both taxonomic and biological in character. At the universities of Michigan and Minnesota, the forest-insect studies have been for the most part ecological in character. At Syracuse University, A. H. MacAndrews is in charge of the forest entomological work. He succeeded M. W. Blackman when the latter became associated with the Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture. The forest entomological research at Syracuse has been both taxonomic and biological.

At Connecticut State College, forest-insect studies have been conducted for many years by various workers. At present, R. B. Friend is actively carrying on studies of forest insects, especially those concerned with second-growth timber and plantations.

Several important forest-insect investigations have been conducted at the Harvard Forest by members of the staff and students. Much of this has been in cooperation with the Bureau of Entomology and Plant Quarantine. H. B. Pierson, now state forest entomologist of Maine, conducted his studies of the white-pine weevil and the pales weevil at the Harvard Forest.

This discussion of contemporary forest entomology is by no means complete, but it will provide a general idea of where and by whom some of the more important activities are being conducted in the United States. Examination of current literature will add to the information presented here.

In Canada the Forest Insect Division of the Entomological Branch is responsible for the major part of the forest-insect work conducted in that country. This division is under the direction of J. J. de Gryse. Like the work in the United States

that in Canada is in large part conducted at field laboratories. No attempt will be made here to list these laboratories or to discuss their work. In the East, however, the work of R. E. Balch deserves special mention. One of the chief projects of his laboratory is concerned with the European spruce sawfly. In the West the work of Ralph Hopping has been chiefly on bark beetles and borers.

The Dominion Parasite Laboratory at Belleville, Ont., in charge of A. B. Baird, cooperates in the introduction and establishment of parasites, particularly those of introduced insects.

CHAPTER III

BIOTIC POTENTIAL

The actual abundance of forest insects in general and of any one species in particular will depend upon their ability to multiply and to live, in spite of the various destructive forces in their environment. Before it can be ascertained what the actual abundance of any insect will be, one must take into careful consideration, in the first place, the ability of that insect to multiply in the absence of any destructive force and, in the second place, the value of the sum total of all the environmental forces working toward destruction. In other words, life is the result of a struggle between the forces of potential creation and potential destruction. Chapman (1925) has proposed apt terms for these two opposing forces, namely, *biotic potential* and *environmental resistance.*

The factors which enter into the composition of these two forces will be discussed under the preceding terms in two separate chapters. The relationship of the two forces to one another in determining insect abundance will be left to a third chapter.

THE RATE OF MULTIPLICATION

The biotic potential[1] of an insect species is its ability to multiply in a given time when relieved of all environmental resistance. It depends upon the rate of multiplication and the sex ratio. The rate of multiplication, in turn, is determined by an insect's fecundity and the length of the developmental period. At this point it should be made clear that the force of biotic potential alone does not determine the population level that a species will reach, but merely the rate of increase that will occur in the absence of environmental resistance.

[1] The term *biotic potential* as used here is synonymous with *reproductive potential* of Chapman (1925). *Survival potential* as used by Chapman has proved to be a confusing term and is therefore not used in this book. Protection against environmental resistance (*survival potential* of Chapman) is discussed in Chap. V.

Fecundity.—The ability to produce young is one of the basic factors determining biotic potential. Among insects there is a wide range of variation in this ability. The number of eggs that may be deposited by a single female may vary from a very few, as is the case with some wasps, to hundreds of thousands, as with the termites.

In general, the fecundity of insects is relatively high. Folsom (1922) quotes Mauw to the effect that two females of the broad-necked root borer, *Prionus laticollis*, were found to have in their ovaries 332 and 597 eggs, respectively. He further cites Girault as authority for the following data concerning the fecundity of certain species:

	Maximum	Minimum	Average
The evergreen bagworm, *Thyridopterix ephimeræformis*	1,649	465	941
The apple-tree tent-caterpillar, *Malacosoma (Clisiocampa) americana*	466	313	375.5
The scurfy scale, *Chionaspis furfura*	84	33	66.5

Other investigations have shown that the white-pine weevil, *Pissodes strobi*, lays on the average 115 eggs per female (Graham, 1926); the spruce budworm, *Archips fumiferana*, 316 (Graham, 1936); the forest tent-caterpillar, *Malacosoma disstria*, about 300 (Fig. 12). Counts made by the author's class in forest entomology showed that the scurfy scale, in the season of 1926 in Minnesota, laid an average of 25.6 eggs per female, with a maximum of 52 and a minimum of 6. This is a considerable variation from the figures cited above. In the same year the oyster-shell scale, *Lepidosaphes ulmi*, produced on the average 27.4 eggs per female, with a maximum of 68 and a minimum of 20, and the white-marked tussock-moth produced on the average 231.8 eggs per female with a maximum of 467 and a minimum of 174. High as these figures are, it is improbable that in any of these cases the maximum possible number of eggs was deposited. For instance, dissection and examination of a series of tussock-moth females showed an average of 476 fully developed eggs per female, with a maximum of 764 and a minimum of 202; much higher figures than those based on counts of the eggs actually deposited.

Polyembryony.—Some insects possess an ability that very materially increases their capacity to produce young. This is called *polyembryony*. It occurs commonly among small hymenopterous parasites, notably the Braconidae and Proctotrupidae. A single egg deposited by a polyembryonic species produces from several to many individuals (Fig. 13). Such a species, although it may produce comparatively few eggs, may still have a high rate of fecundity.

Fig. 12.

Length of Developmental Period.—The rate of multiplication is dependent not only upon fecundity but, also, upon the length of time required for the completion of each generation. Many insects develop slowly. Certain species of Cerambycidae, for example, *Monochamus confusor*, the large pine-sawyer, require under the most favorable conditions a full year to complete a generation, and as many

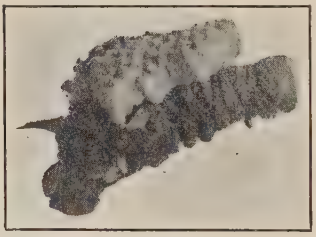


Fig. 13.

Fig. 12.—An egg mass of the forest tent-caterpillar on an aspen twig. Note that the ends of the cluster are cut off rather abruptly. This characteristic will distinguish the egg mass of the forest tent-caterpillar from other closely related species of tent caterpillars.

Fig. 13.—A mass of cocoons of a small hymenopterous parasite, spun upon the body of a dead sphinx larva. The 40 or 50 parasites contained in these cocoons originated from only a few eggs. This illustrates the results of polyembryony. (*University of Minnesota.*)

as 4 years under adverse conditions. Some cerambycid beetles, such as *Hylotrupes banjulus* and *Eburia quadrigeminata*, may live as larvae and pupae for as long as 18 to 20 years. It must be admitted that such extremely long developmental periods are unusual even among wood borers and are the result of unusually adverse conditions. A few insects, however, for example, the periodical cicada, have a normal life cycle almost as long as this.

On the other hand, some of the fruit flies of the genus Drosophila, under favorable conditions, may complete their development from egg to adult in less than 2 weeks, and we may thus have from 10 to 20, or even more, generations per year. Thus the short life cycle of such insects, coupled with the high fecundity of the individual insects, makes possible a rate of multiplication too great for the mind to comprehend. As an illustration of these tremendous possibilities the calculation of LeFroy (1909) concerning the unrestricted multiplication of Drosophila may well be cited. He calculated that a single pair of fruit flies, if all their progeny lived and in turn reproduced themselves under favorable conditions, would in one year produce a mass of flies that, if packed 1,000 to the cubic inch, would cover the entire area of India to a depth of 100,000,000 miles or would cover the earth to a depth of 1,000,000 miles. Such a potential seems almost beyond belief since, owing to the effects of environmental resistance, the complete realization of such a possibility may never be seen. Nevertheless, the immense possibilities of multiplication must not be overlooked.

SEX RATIO

The next of the important factors determining the biotic potential of a species is the proportion of males and females that is characteristic of the species. This proportion is determined, in part at least, by the habits of reproduction.

Habits of Reproduction.—Sexual reproduction is the type most commonly found among insects, although either partial or complete parthenogenesis is characteristic of many species. This latter habit of reproduction occurs very commonly among the Hymenoptera. That important forest pest, the larch sawfly, *Pristiphora ericsonii*, is partly parthenogenetic, as is also the recently introduced European spruce sawfly, *Diprion polytomum*. So also are plant lice, which give birth parthenogenetically to many generations of agamic females. In this way, many more individuals are produced during a season than would be possible under sexual reproduction.

In general, the females predominate in parthenogenetic species. This holds true in the case of the larch sawfly, which has 96 females to 4 males. With such a high proportion of females the number of progeny resulting from any one generation of this

species is much greater than would be the case under the usual proportion of the sexes, that is, approximately one-half males and one-half females. The *sex ratio* must be taken into consideration in calculating biotic potential. The term *sex ratio* has been used in several ways. Frequently it indicates the ratio of males to females. More recent usage, where mathematical computations are involved, expresses the *sex ratio* as the ratio between females and the total population. This latter expression had better, for the sake of clarity, be called the *sex factor*. The sex factor of a species is determined by dividing the number of females in a given group by the total number of individuals in that group. Thus, if the sexes occur in equal numbers, the sex factor will be 0.5. In a purely parthenogenetic species, in which no males occur, it will be 1.0. In the case of the larch sawfly, mentioned above, the sex factor is 0.96.

The Effect of Sex Factor.—The important part that the sex factor plays in determining the biotic potential of a species may be illustrated by a simple calculation comparing two hypothetical insect species, one of which produces equal numbers of males and females, while the other produces only females. We will assume that each of these species lays 100 eggs per female. If we start with two individuals of each species and calculate the rate of multiplication for each through five generations of progeny, assuming that each female lays her full quota of eggs and that every egg produces an adult individual, we shall see a great difference in the final numbers for each species.

Hypothetical Young Produced during Five Generations

Generations		First	Second	Third	Fourth	Fifth
Species No. 1	Males 1..	50	2,500	125,000	6,250,000	312,500,000
	Females 1	50	2,500	125,000	6,250,000	312,500,000
	Totals....	100	5,000	250,000	12,500,000	625,000,000
Species No. 2	Males 0..	0	0	0	0	0
	Females 2	200	20,000	2,000,000	200,000,000	20,000,000,000
	Totals....	200	20,000	2,000,000	200,000,000	20,000,000,000

In the fifth generation, it will be seen that species Number 1, in which the males and females are of equal number (a sex factor

of 0.5), has reached a total of 625,000,000 individuals, while species Number 2 composed solely of females (a sex factor of 1.0), has a total of 20,000,000,000. Thus, it is evident that sex factor is of vast importance in determining biotic potential, because it expresses the numbers of individuals in each generation of a species that are capable of producing new individuals.

THE CALCULATION OF BIOTIC POTENTIAL

Unless a specific numerical value for the biotic potential of a species can be assigned, the term can have little or no practical significance. Until now it has been impossible to arrive at such a value because the knowledge of the factors concerned has not been sufficient.

In order to calculate the value of the biotic potential of a species, all the factors that have just been discussed must be taken into consideration. The number of ovules that a single typical female is capable of producing, the number of generations that will be produced in a given time under optimum conditions, and the sex factor must all be known. The values for these factors are, so far as known, practically constant for any species of insect existing under ideal conditions, and they are sometimes called the constants for that species. If these constants are known, then the biotic potential of any species may be calculated.

Values for Fecundity.—Since, according to the definition, these constants represent values for factors when the insect species is under ideal conditions, any statistics obtained from insects living under ordinary natural conditions, which are usually not ideal, cannot be taken. In the case of fecundity, for instance, it is not the number of eggs which a typical female of a species actually lays that is the constant for that species but the number she is capable of laying. To secure this potential number several methods may be used. The most accurate would be to rear a number of females from eggs to adults under ideal conditions, count the total egg production of each, and use the average egg production under ideal conditions as the potential fecundity. Although this method has been used in several instances it is difficult and time consuming; therefore some easier way is desirable.

One method that is easier but, unfortunately, not so accurate is to count the fully developed eggs in the ovaries of gravid

females that have never laid eggs and assume the maximum number found in any one female to be the constant for that species. The reason for taking the maximum rather than the average, in this instance, is because in nature every individual is subject to the action of environmental resistance and therefore even the maximum is probably lower than the actual potential fecundity. This method gives an approximate value for fecundity which may be used tentatively for those insects that lay their full quota of eggs within a few days. It cannot be used as an index of fecundity in species having a long period of oviposition, because such species continue to mature eggs throughout their lives.

Observing the number of eggs laid in confinement seems to be the only feasible method that can be used for insects that oviposit over a considerable period. Preferably this confinement should be under ideal conditions when, as indicated above, the average production would be used. But if the optimum is not attainable then it would be logical to assume that the maximum oviposition observed represented more nearly the potential fecundity.

Values for Other Factors.—The values for the other factors that enter into the calculation of biotic potential are more easily obtained. For instance, the determination of the sex factor may be accomplished by rearing a large number of individuals and determining the number of each sex in the group. The number of generations in a given period and the number of individuals produced from a single egg may also be determined by simple rearing experiments. Chapman, in the calculation of biotic potential, has used with adaptations a mathematical formula, proposed by Thompson (1922) to express the number of progeny that will result from a given population in any number of generations. In this formula p represents the original population, which in the calculation of biotic potential will be a single individual, z represents the product of the number of eggs per female and the sex factor, and n represents the number of generations in a given time. Then the number of progeny in n generations is pz^n. This formula is sound except when dealing with species that are polyembryonic, in which case it is necessary to include that factor also. For instance, if y represents the number of progeny arising from a single egg, the formula will then read $p(zy)^n$.

For example, if it is assumed that the egg-laying capacity of the white-marked tussock-moth is 764 eggs per female (the maximum number of fully developed eggs recorded as found in gravid females), the sex factor is 0.5, the number of individuals produced from an egg is 1, and the number of generations per year is 1; then the annual biotic potential for the species, expressed for a single insect is $1 \times (382 \times 1) = 382$. If, however, this were a polyembryonic species producing 4 individuals from a single egg, and if it passed through two generations per season, the biotic potential would be $1 \times (382 \times 4)^2 = 2{,}334{,}784$.

This simple calculation demonstrates clearly the importance of each of the various factors of biotic potential. Fortunately for man, this stupendous potential of creation is held in check by the forces of destruction that will be analyzed in the following chapter.

CHAPTER IV

ENVIRONMENTAL RESISTANCE

Environmental resistance is the sum of all the factors in an environment that tend to reduce the rate of insect multiplication. The factors that are combined to produce this force, so far as forest insects are concerned, may be divided into four principal groups: physical, nutritional, plant physiological, and biotic. These groups will be considered separately.

PHYSICAL FACTORS

Perhaps of all the limiting factors of the insect's environment the physical group has received the most intensive study and is best understood. But the knowledge of even this group is still far from complete. It is known in general that temperature plays an important role in determining the rate of insect development and also the possible distribution of all insects, but there are comparatively few species the temperature reactions of which are definitely known. Likewise, the effects on all species of light, moisture, air movement, and all the other factors that are thought of in connection with climate and weather are far from fully understood. Nevertheless, much important progress has been made along these lines. In the following pages some of the more important effects of the action of these physical factors upon insect activities will be discussed.

Temperature.—One of the most important physical factors that regulate insect activity is temperature. Each species of insect has a definite range of temperature within which it is able to live. Temperatures above or below this range result in the insect's death. Near the upper and the lower endurable limits are the dormant zones in which all external movement ceases. When an insect is in the lower of these zones, it is said to be in hibernation; when it is in the upper zone, it is said to be in a state of estivation. Between these dormant zones lies the zone of activity or, as it is sometimes called, the *zone of effective temperature.*

As the temperature rises above the zone of hibernation in the effective zone, it becomes more and more favorable for insect development until an optimum point is reached. As the temperature rises above the optimum, conditions become less and less favorable, until all activity ceases when the zone of estivation is reached.

The temperature requirements of insects vary with the species. Some species are active at a temperature only slightly above the

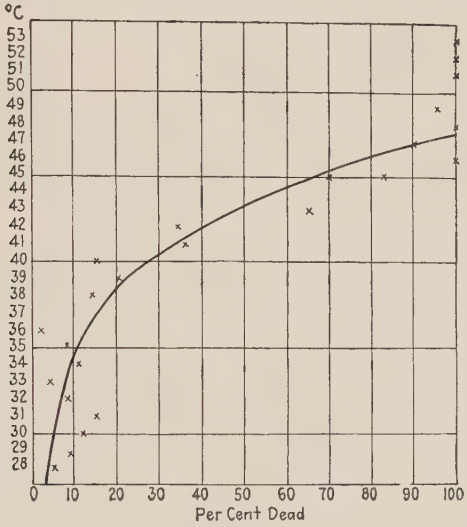


FIG. 14.—Graph illustrating the effect of high temperature upon adults of the balsam-fir bark-beetle, *Pityokteines sparsus*. The temperatures are subcortical and are, of necessity, only approximate. Practically none of the beetles are able to survive a temperature higher than 48°C.

freezing point of water, whereas most species are active only at temperatures above 15°C. The optimum temperature for most insects is in the neighborhood of 26°C., and estivation usually begins at from 38 to 45°C. For many insects, 48°C. (Fig. 14) is the point of fatality at high temperatures, although some of the heat-resistant forms, for example Chrysobothris, can endure a temperature of 52°C. for a short period (Graham, 1922). The low fatal temperature varies both with the species and with the season. It has been shown that the same species is able to endure much more cold in the fall and winter than in the spring and summer (Payne, 1926). The width of the zone of hibernation is so variable that no general statement regarding the usual point of

FIG. 15.—Life zones of Merriam. (*Biol. Survey, U. S. Dept. Agr.*)

fatality at low temperature can be made. All that can be said is that tropical species are, as a rule, much more susceptible to cold than are the temperate species.

This brings us to a consideration of the influence of temperature factors upon the distribution of insects. Several more or less successful attempts have been made to determine life zones on the basis of the sums of effective temperatures for different localities. Merriam (1898) used this basis for the construction of the life zones that are generally used in biological work (Fig. 15). Sanderson (1908) has shown, however, that insects do not always occur in every locality where the total of effective temperature is sufficient to make possible their complete development. Thus even though there may be a sufficiency of warm weather in the summer, a species may be kept out of a locality as a result of extremes of cold in the winter. For instance, the northward distribution of the gypsy and the brown-tail moths is definitely limited by low winter temperatures (Summers, 1922), and it is probable that owing to this neither of these insects will ever reach the northernmost point at which summer temperatures are favorable.

A very useful empirical law has been developed by Hopkins (1920, 1921, and 1938) which is known as *Hopkins's bioclimatic law*. By the use of this law it is possible to prophesy from known conditions in one locality what conditions will exist at the same time in another locality. According to this law any periodical biological phenomenon—such as the emergence of insects from hibernation, the spring awakening of vegetation, or the entrance of insects into hibernation—is correlated with latitude, longitude, and altitude. The law may be stated as follows: Other conditions being equal, the variation in time of any seasonal event in temperate North America occurring in the spring and early summer is at the general rate of 4 days later for each degree of latitude northward, or 5 degrees of longitude eastward, or 400 feet of altitude upward. In the late summer and fall, conditions are reversed. This law appears to hold reasonably well for at least those portions of temperate North America east of the Rocky Mountains. Consideration of this law shows clearly why, on the basis of temperature alone, a high mountain range might prove an impassable geographical barrier to the spread of animals or plants from one region to another.

In the preceding discussion we have seen how temperature limits the geographical distribution of insects. It also limits with equal certainty the local distribution of these animals. The local temperature varies greatly within very short distances. For instance, on a bright day in summer the temperature at the surface of the ground may be as much as 50°C. higher than the air temperature at breast height. A difference of from 10 to 20°C. between surface temperature and the temperature one foot above the surface is not at all uncommon. With such a wide

A *B* *C*

FIG. 16.—Variations in the amount of insect work on three sides of a white-pine log lying in full sunlight. *A* shows the sterile zone on the top side where high temperatures prevail. *B* shows the bottom side which is too moist and cool for many insects. *C* shows that on the side section, where conditions are ideal for the maximum number of species, insect galleries occupy most of the area.

range within such a limited space, it is possible for many insects to change their position so as to keep within a favorable zone (Chapman, 1925).

Some insects, those living in logs for instance, are unable to move quickly from place to place. If they happen to be working on the upper side they cannot move away from that location in the event that conditions become unfavorable. Likewise, if they are working on the lower side they must face what comes in that location. If conditions become sufficiently unfavorable, the insects may be killed (Figs. 16*A*, 16*B*, and 16*C*). In logs having comparatively thin dark-colored bark the side exposed to direct

solar radiation may reach 60°C. (Fig. 17) or more (Graham, 1922 and 1924). Such temperatures are far above the fatal point for all insects, and so on the upper side of logs lying in the sun there is usually a sterile zone. On the sides where favorable temperatures prevail, the insects occur in greatest numbers; while on the lower side, where uniformly cool conditions are found, there exist only those species that are able to live under cool

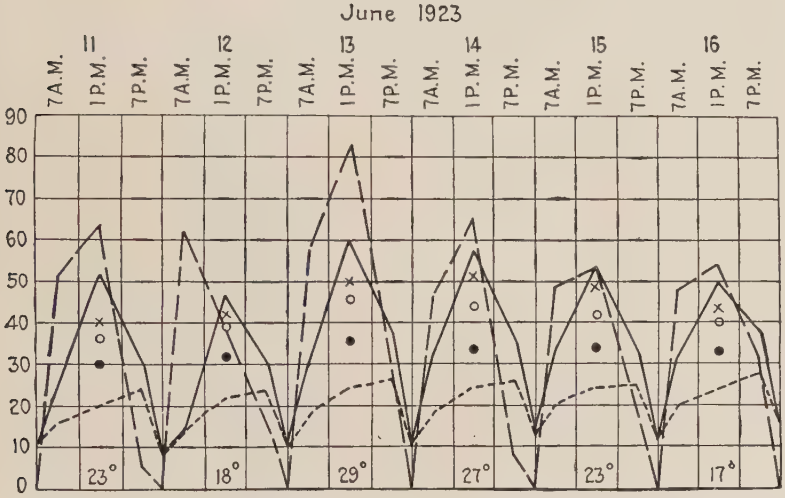


FIG. 17.—Graph illustrating the daily fluctuation of subcortical temperature, expressed in degrees Centigrade, on the upper side of white-pine logs lying under different light conditions. Subcortical temperature in full sun is represented by the solid line; in full shade by the short dashes. The subcortical temperatures at noon for logs in two-third sun, one-half sun, and one-fourth sun are indicated by the cross, the circle, and the dot, respectively. Daily fluctuations in subcortical temperature are due chiefly to fluctuations in air temperature and light intensity. Air temperature at noon is indicated in degrees Centigrade along the bottom edge of the graph; light intensity by the broken line. Note the variation in the effect of these factors under different shade conditions.

conditions. The fatal effect of high temperature upon log-inhabiting insects is made use of, as will be shown later, in insect control.

Temperature not only affects the geographical and local distribution of insects but also regulates the rate of insect development (Fig. 18). In general, the rate of development increases in proportion to the increase in temperature until the point of optimum temperature is reached. The rate of this increase varies somewhat at different temperatures and with different species, but, in

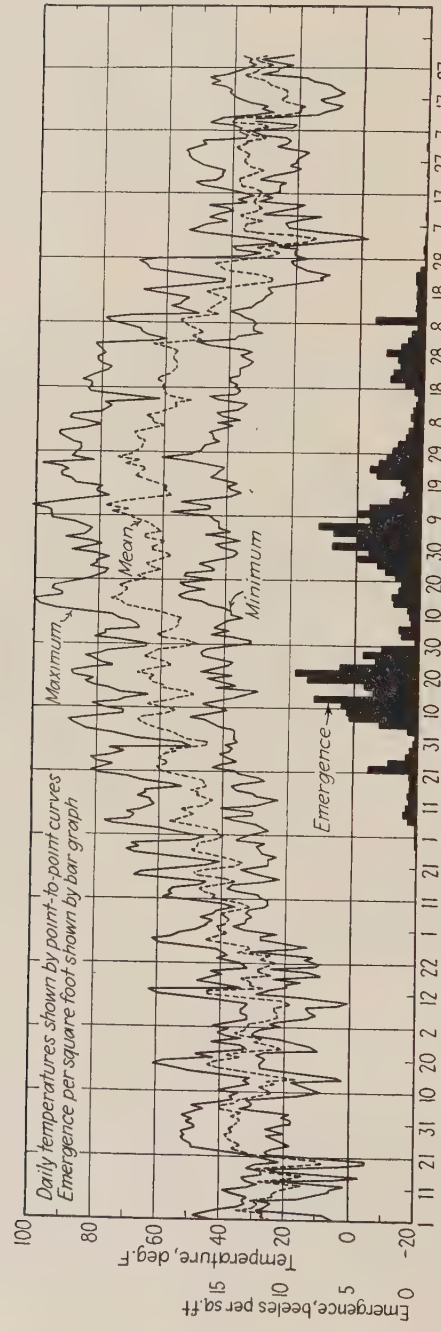

Daily temperatures shown by point-to-point curves
Emergence per square foot shown by bar graph
Maximum
Mean
Minimum
Emergence
Temperature, deg. F
Emergence, beetles per sq. ft
Jan Feb Mar Apr May June July Aug Sept Oct Nov Dec

FIG. 18.—Temperature and the emergence of *Dendroctonus brevicomis*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

general, an increase of 10°C. doubles the rate of development. Sanderson and Peairs (1913), Peairs (1927), Krogh (1914), and other workers have expressed the increase in velocity of development more accurately, stating that the rate of development increases directly with the temperature, the developmental curve being a segment of a true mathematical hyperbola. Since the reciprocals for the points on a hyperbola fall, by definition, in a straight line, then if we plot the reciprocals of two points and connect them by a straight line, it will be possible to compute the rate of development at any other temperature. Above the optimum point a reduction in rate of development occurs with increasing temperature, until at a high temperature the rate of development is reduced to zero. The seasonal activities of many insects are definitely regulated by temperature. The number of generations and the time of emergence (Fig. 18) are both correlated with temperature conditions.

Light.—The reactions of insects to light are not very different from their reactions to temperature, and, since these factors are usually closely associated with one another, and since they generally vary synchronously, it is often difficult to determine whether the effects are produced by the one or by the other.

Theoretically, it seems possible to divide light, just as we do temperature, into optimum, effective, lethal, and fatal zones. Inasmuch as some insects respond positively and some negatively to light, it may be assumed that the optimum must vary greatly with different species. The stimulating effect of light on certain species is well illustrated by the reaction of Chrysobothris adults. These beetles remain inactive on cloudy days when the air temperature may be as high as, or higher than, the temperature on some sunny days when they are active. Carpenter (1909) has shown that the convulsive motor reactions of Drosophila, which normally occur at a temperature of 39°C., appear at 30°C. under the rays of a strong light of 480 candle power. Although certain insects are not able to endure strong light, it seems probable that light under natural conditions rather seldom goes beyond the limits of toleration of most species. It is true, however, that the presence or absence of light determines to a greater or less extent the local distribution of insects. Those that are positively phototropic or heliotropic will be found for the most part in the open, whereas those that respond negatively

will be found in the soil, under rocks or bark, or in some other dark location. In some instances light appears to be an important factor in determining the place of oviposition of certain insects. For instance, Chapman (1915) has shown that the two-

FIG. 19.—Red oak trees standing in full sunlight are especially susceptible to injury by Agrilus. (*University of Minnesota.*)

lined borer, *Agrilus bilineatus*, deposits its eggs by preference upon trees exposed to full sunlight (Fig. 19). This is apparently also true of the bronze birch-borer, *Agrilus anxius*. From this discussion we see that light is difficult to separate in its effects from temperature, but there is good evidence to indicate that this factor is important in the life of insects.

Moisture.—Another physical factor of the environment that plays an important part in insect activity is moisture. As with all other forms of life, so it is with insects: both their distribution and development are dependent on the presence of water in the environment. The effectiveness of heat in stimulating or retarding the velocity of insect development is also influenced by the amount of moisture present. Under favorable moisture conditions an insect is not so susceptible to extremes of temperature as it would be under unfavorable moisture conditions (Pierce, 1916) (Fig. 20).

With moisture, as well as with temperature, each species has definite requirements with optimum and effective zones. The extreme zones (lethal or fatal) are less clearly marked than is the case with heat. Under ordinary conditions, an excess or deficiency of moisture does not result in an insect's immediate death but only in a disturbance of its activities. There are, however, certain outstanding instances of forest insects that are definitely limited in their activities by the moisture factor. The powder-post beetles, for instance, cannot live in moist wood (Synder, 1926), whereas the ambrosia beetles cannot develop in dry wood. The rate of development of other wood-boring species may be greatly reduced by the desiccation of the wood. In fact, there are cases on record in which a wood borer having a normal life cycle of 1 or 2 years has required, because of unusually dry conditions, 20 years or more to reach maturity.

Climate and Weather.—In view of the important effect that any one of these factors of temperature, light, or moisture may have on the life of forest insects, it is evident that, when all three are combined and joined with still other factors, the resulting complex, which we call weather or climate, must be of fundamental importance in considering forest-insect problems. Climate is the result of the combined action of all the physical factors of the environment over a long period of time and, so far as meteorological evidence is concerned, appears to be relatively stable in the same locality. It forms the basis of Hopkins's bioclimatic law and of Merriam's life zones.

Weather, on the other hand, is the result of the combined action of all the physical factors of the environment at any given time, and it varies from hour to hour, day to day, and week to week. It influences the abundance of insects and the rate of develop-

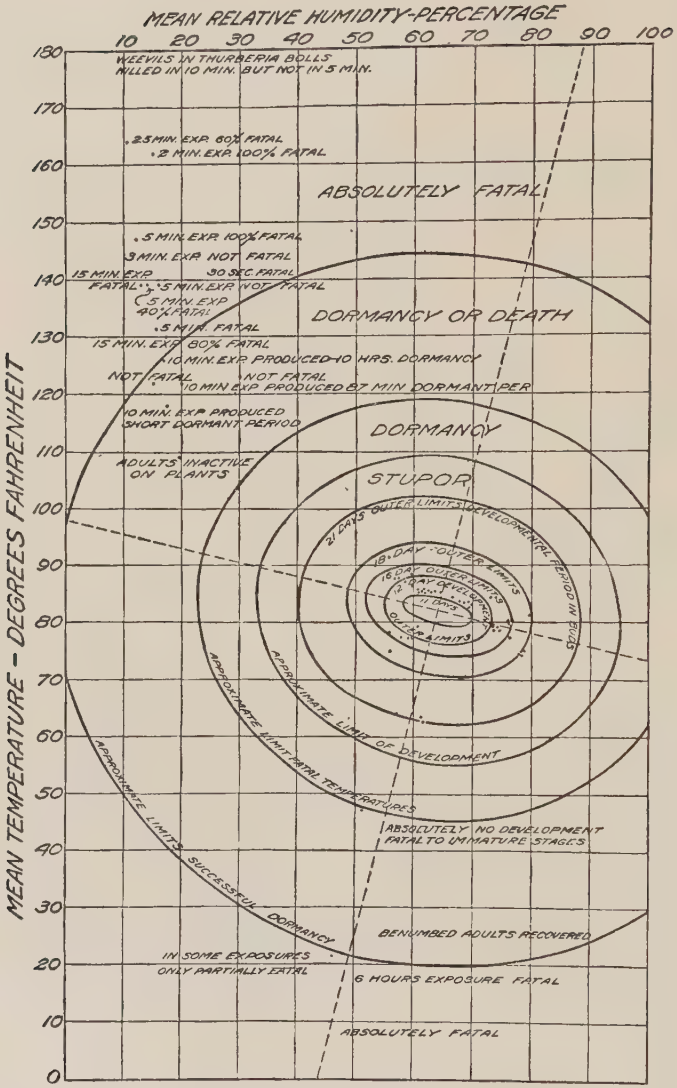

MEAN RELATIVE HUMIDITY-PERCENTAGE
10 20 30 40 50 60 70 80 90 100
MEAN TEMPERATURE - DEGREES FAHRENHEIT
180 170 160 150 140 130 120 110 100 90 80 70 60 50 40 30 20 10 0
WEEVILS IN THURBERIA BOLLS KILLED IN 10 MIN. BUT NOT IN 5 MIN.
.25 MIN. EXP. 80% FATAL
.2 MIN. EXP. 100% FATAL
ABSOLUTELY FATAL
.5 MIN. EXP. 100% FATAL
3 MIN. EXP. NOT FATAL
15 MIN. EXP. FATAL
30 SEC. FATAL
5 MIN. EXP. NOT FATAL
5 MIN. EXP. 40% FATAL
.5 MIN. FATAL
DORMANCY OR DEATH
15 MIN. EXP. 80% FATAL
10 MIN. EXP. PRODUCED 10 HRS. DORMANCY
NOT FATAL
10 MIN. EXP. PRODUCED 87 MIN. DORMANT PER
10 MIN. EXP. PRODUCED SHORT DORMANT PERIOD
DORMANCY
ADULTS INACTIVE ON PLANTS
STUPOR
21 DAYS OUTER LIMITS OF DEVELOPMENTAL PERIOD IN FRUIT
18 DAY OUTER LIMITS
16 DAY OUTER LIMITS
14 DAY OUTER LIMITS
12 DAYS
11 DAYS
OUTER LIMITS
APPROXIMATE LIMIT OF DEVELOPMENT
APPROXIMATE LIMIT FATAL TEMPERATURES
ABSOLUTELY NO DEVELOPMENT FATAL TO IMMATURE STAGES
APPROXIMATE LIMITS SUCCESSFUL DORMANCY
BENUMBED ADULTS RECOVERED
IN SOME EXPOSURES ONLY PARTIALLY FATAL
6 HOURS EXPOSURE FATAL
ABSOLUTELY FATAL

FIG. 20.—Graph showing the combined effect of temperature and relative humidity upon the activity of the cotton-boll weevil. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

ment from year to year, and from season to season, in every locality. With insects of the forest, as well as with others, weather conditions are exceedingly important in regulating abundance. A late frost in the spring after the eggs of the forest tent-caterpillar have hatched may result in the starvation of almost all the young larvae of that species (Blackman, 1918). The same thing is true of all leaf eaters that feed upon deciduous trees in early spring. Heavy rains during the larval stage of insects that feed on the exposed surfaces of trees may wash off and destroy large numbers of such insects and thus reduce the possibility of their becoming epidemic. Cool weather during the developmental period may so lengthen the larval or nymphal stage that a much larger proportion of the species may fall prey to their enemies than would otherwise be the case. Also moist warm weather may make possible outbreaks of entomophagous organisms such as disease-causing bacteria or protozoa. On the one hand, dry weather may so reduce the vegetative growth of trees on which certain species feed that great injury results from the activities of only a normal number of pests, or, on the other hand, an unusually luxuriant growth may overcome effects of an insect attack that might in the average season produce great injury to the trees. In the case of most defoliating insects, high temperatures combined with light rainfall tend to favor insect development and to encourage outbreaks.

The various physical factors discussed above may be much better understood than any of the other limiting factors of the insect environment, but it would be erroneous to assume that there are not other factors equally important entering into environmental resistance. These will be discussed under the headings of nutritional, plant physiological, and biotic factors.

NUTRITIONAL FACTORS

The physical factors of the environment do not lend themselves to regulation, whereas the nutritional factors may often be controlled with a reasonable degree of exactness. If the food conditions can be so controlled that outbreaks of pests are improbable even with weather favorable for insects, then we can cease to disturb outselves concerning the effects of weather upon the rate of insect multiplication. For this reason, if for no other, we should be particularly interested in the nutritional factors.

Quantity of Food.—It is an accepted biologic law that, other things being favorable, an organism will eventually multiply to the limit of its food supply. As a rule, the more numerous the individuals of a tree species, the more abundant are its insect

FIG. 21.—Tussock moth, *Hemerocampa osleri*, from Inyo National Forest. An insect which attacks pure or nearly pure forests. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

enemies. When there is an unlimited and convenient supply of a certain species of trees, then the stage is set for an outbreak of the insect pests of that tree (Fig. 21).

The spruce budworm outbreaks in eastern United States and Canada, as will be shown later, are associated with an overabundance of balsam fir, and possibly white spruce. Similarly, the larch-sawfly outbreaks have undoubtedly been stimulated by large volumes of tamarack, and forest-tent-caterpillar out-

breaks by extensive stands of poplar or other suitable food trees. Our forest and shade trees are often listed according to their susceptibility to insect attack. On examination of these lists it is found, with rare exceptions, that the species listed as insect resistant are those which do not occur commonly in large masses. Norway or red pine is usually classed as insect resistant, but accurately speaking it cannot be said that this and similar species are any more resistant than other species. Their apparent resistance is due to their relative scarcity in the forest. It is quite certain that if the proportion of these species were greatly increased, some of the many insects that now occur upon them in innocuous numbers would become serious pests.

Fig. 22.—A jack pine more than 80 per cent defoliated by the spruce budworm and the jack-pine sawfly working together. This sort of injury is common where jack pine occurs over large areas.

At one time, jack pine was regarded as an insect-resistant species, but now it is being seriously attacked by a number of dangerous pests (Fig. 22). The reason for this apparent change in susceptibility may probably be explained by the fact that in the range of the jack pine this species has largely replaced the white and norway pine, which a few years ago formed the major portion of the virgin forest in the Lake states. This has meant a tremendous multiplication in the quantity of jack pine. Today instead of only scattered blocks of jack pine on lands too poor to support other species, we have vast areas over which this species is predominant. Thus the quantity of food available becomes an important factor in regulating insect abundance.

Kind and Quality of Food.—The abundance of forest insects and the length of the developmental period are also limited by the

kind and quality of food that they are able to use. An insect species, for instance, that feeds only on the succulent tissues of the phloem must complete its feeding period quickly while the perishable material upon which it feeds is still in usuable condition. Although perishable, this food is comparatively high in food value. We should expect, therefore, that the phloem region would be filled with an abundance of insects, each with a

FIG. 23.—Work of the spruce budworm on a young jack-pine shoot. The larvae of this insect must complete their growth while the young needles are soft and succulent. Note that the tree on the left has been severely attacked whereas that on the right is practically normal. The current year's injury is indicated by the webbed and matted needles on the injured tips, and defoliation of previous years by the sparseness of the old needles. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

short developmental period, and this is exactly the condition that exists there.

By the nature of their food, leaf-eating species are, with a very few exceptions, limited to a single season or even to a short part of one season for their development. Few leaf eaters can pass the winter as partly grown larvae; consequently they must complete their development before the leaves drop in the autumn. In some cases the length of the developmental period is limited to a few weeks during which the foliage is soft and succulent (Fig. 23).

With the wood borers, on the other hand, feeding as they do upon a medium that changes very slowly, it is not at all uncommon to find their life cycle extending over several years. Many of the wood-boring species, like some of Cerambycidae and

Buprestidae, feed for a time in the phloem before entering the solid wood. In this way the young larvae are provided with more nourishing and more easily digestible food than are the larger larvae. This suggests that the powers of digestion of these species are better in the later than in the earlier stages. Other insects, like the Siricidae, are able to digest solid wood from the earliest stages and are exclusively eaters of solid wood.

On the basis of these facts, it is seen that all tree insects do not have the same food requirements: some require leaves, some find the phloem region to their liking, and still others are able to wrest their living from the solid wood. As the wood is worked over by insects and fungi, its chemical and physical characters change, and with this change new species of insects replace those which attacked the living tree or recently cut log. These in turn are replaced by others until in the last stage of decomposition the population is identical with that of the duff stratum of forest soils. Thus there is a continuous succession of insect species inhabiting the tree from the fresh green condition of the newly felled or killed tree to the completely decomposed condition.

During the process of disintegration there is, in many instances, a close relationship between fungi and insects. In some cases, particularly in the early stages, a true symbiotic relationship can be demonstrated (Baumberger, 1919). Just as the fruit flies can develop normally only where bacteria or fungi are present to aid in the elaboration of raw food, so, in the case of many wood borers, fungi must be present to alter the character of the wood thereby making the food materials available for the insects. In some cases, like that of the ambrosia beetles, the fungus furnishes the entire food of the insect, and the galleries that are cut into the wood by the insects serve only for shelter and a place for the food fungus to grow.

Host Selection.—Most species of forest insects are limited in their feeding either to one species of tree or to a more or less prescribed group of species. The locust borer, for example, feeds only on the black locust, the sugar-maple borer attacks only maples, the larch sawfly defoliates only larch, the Nantucket pine-moth infests only the pines, and the spruce budworm is confined to a comparatively limited group of conifers.

When an insect attacks only one species of tree, its control presents a comparatively simple problem, but when it is a

general feeder, like the gypsy moth, the problem becomes much more complex. Fortunately with many species that feed on a variety of hosts the problem is simplified by the fact that there is a strong tendency for an insect to oviposit on the host upon which it was reared. This is called Hopkins's *host-selection principle* (Craighead, 1921), and it apparently holds true for many of the Cerambycidae and for some Scolytidae. Evidence indicates that it holds true within certain limits for the spruce budworm. Further work along this line may show that this principle may be applied much more generally than is now known to be the case.

Perhaps the operation of this principle has in the past ages given rise to new species by developing first biologic varieties limited to a single host and later to forms distinct morphologically as well. However this may be, whenever host selection occurs, control measures are simplified thereby, because each biologic variety may then be treated as if it were an individual species.

PLANT PHYSIOLOGICAL FACTORS

Trees possess certain physiological characteristics which result in producing, in varying degree, a certain real ability to resist insect attack. These characteristics, by making environmental conditions less favorable for the insect than would otherwise be the case, increase the force of environmental resistance working against the insect.

Rapidity of Growth.—Vigorous trees growing rapidly suffer less from insect injury than do trees of the same species that are growing more slowly. Rapid growth has a double effect in that it actually makes the tree more resistant to both attack and injury. The more rapidly a tree grows, the shorter will be its period of exposure to the series of pests that may attack it during the various stages of its growth. This shortening of each of these stages is in itself a form of resistance, but the rapidly growing tree exhibits still other characteristics that make it less susceptible to attack than its slower growing and less vigorous brothers.

One of these characteristics is the copious flow of sap, or resin, that exudes from wounds of fast-growing, vigorous trees. This flow of resin will drive out, or overwhelm and kill, almost any

of the phloem borers, before they can become established in the tree. Such a tree, except when it is attacked simultaneously by large numbers of these insects, is able to resist attack successfully. In forests where dendroctonus beetles are working, it is not at all uncommon to find trees that have successfully repelled attack, even in the areas of heaviest infestation. Such trees are usually covered with *pitch tubes*, formed by hardened resin that exuded at each point of attack (Fig. 24). Examination of these trees will show the beetles to be entombed in some tunnels in the mass of resin filling their galleries while other tunnels will be deserted.

Other interesting examples of resistance to attack by vigorous growth may be cited. For instance, some of the buprestids sometimes deposit their eggs upon trees that are fairly thrifty. These eggs will hatch and the larvae will penetrate into the bark. In order to develop, these larvae must feed in the inner phloem and cambium for a time at least, but they can feed only on the phloem of decrepit trees or freshly cut logs. Therefore when they reach the inner phloem of a healthy tree they either die immediately or are forced to turn back into the bark where, because they are unable to find suitable food, they die a lingering death. These small buprestid larvae frequently have been found starving in the bark of healthy jack-pine trees.

Not infrequently, other illustrations of the ability of trees to resist attack, owing to their vigor, may be observed. For instance, it is not at all uncommon to find the galleries of phloem insects overgrown by many years of woody growth, indicating an old attack that the tree has outgrown. Galleries of *Agrilus bilineatus*, the two-lined borer; *Agrilus anxius*, the bronze birch-borer; and *Melanophilus californica* are frequently thus overgrown.

Foliage Characteristics.—Sometimes a tree species may resist insect attack because of certain characteristics of its foliage. The lack of synchronization between the spruce budworm and the black spruce illustrates well this kind of resistance. A detailed discussion of this relationship will be taken up later, but it deserves mention here because it illustrates one type of physiological resistance. When the young budworms emerge from hibernation they require tender fresh foliage for food. Their time of emergence is about 2 weeks prior to the opening

FIG. 24.—Pitch tubes on a ponderosa pine that has been attacked by *Dendroctonus brevicomis*. (*Entomological Branch, Can. Dept. Agr.*)

of the black-spruce buds; consequently in a stand of pure black spruce the larvae are faced with a food shortage in the early part of the season. Some of them will find the green tissues that they require by boring into a bud, but many of them will fail to do this and will perish. Thus the black spruce is able to reduce budworm abundance.

The white spruce also has a means of reducing the number of budworm larvae feeding upon it. Unlike the black spruce the buds of the white spruce open at a time suitable for the budworm, but the white-spruce needles harden and become unpalatable before all the larvae reach full growth. Many of them perish when they are forced to leave the trees on which they have been feeding to seek more suitable food. Still another illustration of how a foliage characteristic may prevent the attack of an insect is the way by which the European-elm miner is prevented from attacking the American elm. The leaves of our native elms are much thinner than those of the European species and do not provide enough space to accommodate the miner.

Distasteful Characteristics.—Certain trees apparently possess immunity from insect pests because they are unattractive or actually distasteful to the insects. Just what these characteristics really are is not known but that they exist cannot be doubted. They are often not possessed by all the individuals of a species in the same degree. Some trees may be practically immune to attack while a neighboring tree will be highly susceptible.

A striking example of the variation in this respect is to be observed in a certain plantation of norway spruce in the Saginaw Forest, one of the forest properties of the University of Michigan. This plantation has been rather heavily attacked by an adelgid, often called the *spruce-gall aphid*. Many of the trees are heavily attacked while others are absolutely untouched. Even when the branches of an immune tree interlock with those of a heavily infested tree, the immune tree will remain uninfested.

It is said that certain individual spruce trees in Europe show a decided resistance to the attack of that much dreaded forest defoliator, the nun moth. The larvae refuse to feed upon the needles of these resistant trees but, according to Prell, when branches are cut and placed in water for 24 hours, they will then

be accepted as food. This may indicate that some volatile repellent substance not present in other seeds of the same species neutralizes the native agent that prevents the insect from attacking these resistant individuals.

BIOTIC FACTORS

The fact that environmental factors resulting in death are the multiplication of some insects per fertile female is clear. In this group are included all the interactions existing between the various living organisms in an environment that result in a limitation of multiplication. The biotic factors that play important roles in environmental resistance are competition, predation, and parasitism.

Competition—It is possible for competition to exist either between the individuals of the same species or between different species. The final result in either case is a reduction in the rate of multiplication of the insects concerned. Young insects have a continually acting urge to consume considerable food, water, and shelter. Fig. 2-1, *B* (the three competitive factors) briefly marks this as important. There is normally a more intense and abundant supply of food than all the insects in a locality, as long as the insect is present in epidemic numbers. In larger food, a continuous supply of food be available, only a comparatively small part of that which is in existence at any one time can be used. Food must be produced more rapidly than it is consumed or the supply will eventually be used up. This means that a living race adjusts its supply either organisms which only use a small part of food which is able be produced in excess of its own requirements for maintenance and growth. If the amount of food taken becomes too great, the balance between production and consumption will be temporarily disturbed. This under normal conditions the insects are using only the surplus and not the entire available supply. As result, we can see that there is not enough food and competition for food does exist in other forms of environmental resistance for limiting down the number of individuals to a point where an abundance of food for all exists.

At a time when some insect species may succeed temporarily at the expense of the other forms of life in the forest, by increasing its numbers to a point where all food must be used to meet the

little importance. This type of competition is sometimes very keen among the phloem insects and also among the wood borers. For instance the number of white-pine weevils that can reach maturity in a terminal shoot of a pine sapling is directly proportional to the circumference of the shoot (Graham, 1926). This is due to the feeding habits of the larvae. A single larva working alone would be quickly overwhelmed by the resin that would be exuded into its tunnel by a healthy shoot and would be killed. In order to avoid such a fate the larvae of the weevil work downward side by side, completely encircling the shoot. As they increase in size they become more and more crowded, with the result that the weakest larvae are forced out of line and left to starve, while the strongest forge ahead and are in a short time overwhelmed by resin. The number of full-grown larvae surviving cannot be greater than the number that can lie side by side around the shoot (Fig. 26). Many bark beetles of the family Scolytidae are limited in a similar way. Usually competition is between larvae, but occasionally in cases where all stages of an insect are living in a limited environment, as do the bark beetles and ambrosia beetles, there may be competition between adults and immature stages.

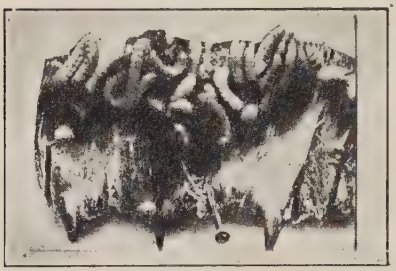


FIG. 26.—White-pine weevil larvae lying side by side as they work downward beneath the bark of the shoot in which they are feeding. Space limits the number that can feed in this way.

Sometimes the abundance of forest insects is limited by competition for suitable shelter. The abundance of termites or of carpenter ants is definitely limited in certain instances by a scarcity of suitable places to build their nests. With most forest insects, however, if food is sufficient, shelter is also available, inasmuch as in the majority of cases the insect's shelter is built either of the food upon which it feeds, or of secretions from its own body, or of a combination of the two (Fig. 27).

Predators and Parasites.—The effect of predators and parasites in producing environmental resistance is so nearly identical that it seems advisable to discuss them together in order to avoid repetition. These two closely allied factors constitute

an important part of environmental resistance. In fact some authorities feel that they are more important than all the other factors combined. Most others, however, do not agree with this estimate of their importance (Howard, 1926), but all agree that without these limiting factors almost all insect species would be much more abundant than they now are.

Both parasites and predators feed upon insects. The chief distinction, in entomological usage, between them is that a parasite obtains its food from a single organism of another species, the host; whereas the predator feeds upon a series of victims, the prey. A parasite, according to the generally accepted definition, obtains its food from its host without killing the host directly. In entomological usage, on the other hand, the host is usually killed. The insectivorous predator, however, always kills its prey. Among the important parasites of insects are representatives of many groups: fungi, bacteria, protozoa, various arthropods including insects, nematodes, and other organisms. Of all these, insect parasites of other insects have received most attention from entomologists. Predators, like parasites, have representatives among many groups of animals. Some of these are birds, mammals, reptiles, amphibians, and not the least important, other insects. No stage in the development of an insect is free from the attack of predators and parasites.

FIG. 27.—A typical bag of the evergreen bagworm. This bag is constructed of silk, spun by the insect, combined with bits of leaves and twigs. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

Even though the eggs of insects are generally very small objects, they nevertheless have both their predaceous and parasitic enemies. No matter how carefully they are hidden away some of them are almost certain to be found and destroyed. Insect eggs furnish a staple item of diet for nuthatches and chickadees (Fig. 28). After watching one of these insectivorous

birds searching the trunk and branches of trees especially during the winter, it is easy to believe that they are extremely effective in reducing the number of insects that pass the winter in the egg stage.

FIG. 28.—A chickadee searching for insect eggs. (*New York State College of Forestry, Syracuse University.*)

The eggs of insects are attacked by parasites as well as by predators. Even the eggs of small moths, like the Nantucket

pine-moth, are sufficiently large to provide food enough for the development of a tiny parasite. During 1926, in the Bessey Plantations at Halsey, Neb., about 60 per cent of the summer generation eggs of this insect were parasitized. Careful examination of the eggs of aphids, tussock moths, tent caterpillars,

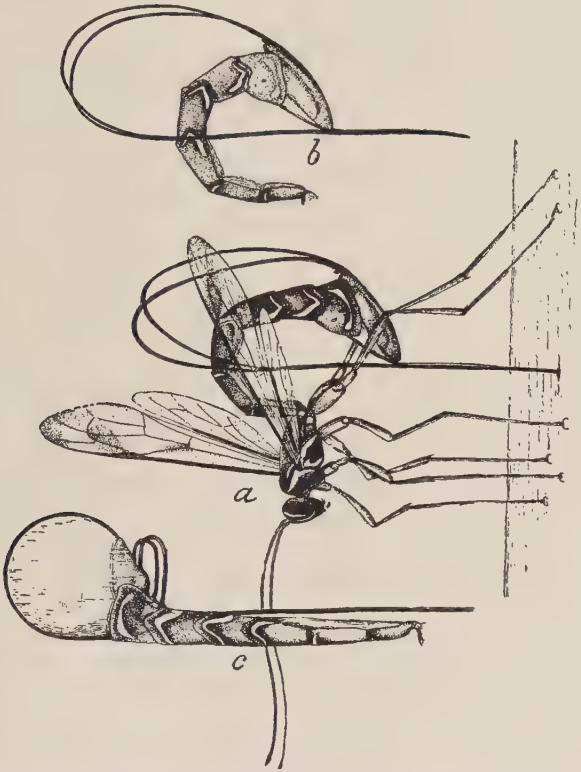


FIG. 29.—*Megarhyssa* (*Thalessa*) *Lunator*, one of the largest of the ichneumon flies. *a* pictures a female in the act of parasitizing a wood-boring larva; *b* and *c* show the details of the ovipositor. (*Bureau of Entomology and Plant Quarantine U. S. Dept. Agr.*)

or almost any other species will reveal the fact that many eggs that have failed to produce larvae are perforated by the exit hole of one or more egg parasites.

In spite of the activity of both predators and parasites in destroying the eggs of insects, there is usually an ample supply of larvae produced to cause a decided increase in the insect abundance, if they were all to complete their development. But, in the larval stage also, predators and parasites operate in such a

way as to hold down the rate of multiplication. Even the larval stages of wood borers, well protected though they are by the wood in which they are tunneling, are not safe. The woodpeckers dig them from their tunnels; some of the ichneumon flies (Fig. 29), by inserting their long ovipositors through the wood, succeed in parasitizing them; and some of the predaceous beetles follow them into their tunnels and there destroy them.

Larvae of defoliating insects, and other insects on the surface of plants, because of their comparatively exposed position, are attacked by a host of enemies too numerous to mention. Insect parasites, predaceous insects, and birds all take their toll. When the larvae drop to the ground either accidentally or, as many do, to prepare for the pupal stage they expose themselves to the attack of the terrestrial predators. Shrews, mice, and skunks are all very fond of insect food and seize hungrily upon any larvae that they find. Ants, also, are not averse to insect food, and feed on small larvae. The great reduction in insect numbers by predators and parasites probably occurs during the larval period.

Insects usually seek secluded places for pupation, and many spin cocoons to protect them during this quiescent period. But careful as they may be to hide or protect themselves, many of them will be found and killed. Parasites of the pupal stage are not common. Predators are, however, sufficiently plentiful. Insectivorous birds and insects feed upon the pupae above ground and small mammals, for example shrews and mice, dig up and eat those in the ground.

Adult insects are attacked by parasitic mites, nematodes, and other parasites but do not usually succumb to the attack of these animals. How much injury the insect suffers from these organisms is not known, but it is quite probable that they are injured to some extent by them. Insect parasites of adult insects are rare. Predators, particularly vertebrate predators, constitute the most important biotic factor of environmental resistance in so far as adult insects are concerned. In addition to the vertebrate predators, however, predaceous insects and spiders kill many adult insects.

From the foregoing discussion it is evident that, inasmuch as predators and parasites attack insects in every stage of their development, they are important factors of environmental resistance.

CHAPTER V

INSECT ABUNDANCE

The importance of insect abundance lies in the fact that the ability of any one insect species to injure trees depends primarily upon the numbers of that insect in a forest.

BIOTIC BALANCE

Most insect species that feed upon the trees in any forest area never occur in sufficient numbers to cause appreciable damage. On the other hand, there are some species that occasionally become extremely abundant and injurious. The latter are the insects that we usually regard as forest pests, the former are usually disregarded.

Nature's Deadlock.—It must be admitted that every insect which can successfully attack a living tree is potentially a menace to that tree. Fortunately, however, under normal conditions no insect species is allowed to multiply so rapidly that it occurs in sufficiently large numbers to injure seriously the trees upon which it feeds. This is evident from the fact that natural forests usually have developed to maturity and have not been destroyed by insects, in spite of the continued presence of hundreds of potentially dangerous species. It is only under abnormal or unusual circumstances that insects become sufficiently abundant to cause outbreaks. Normally, no species is able to dominate the environment at the expense of the others. Each species maintains itself only in moderate numbers, too few to cause appreciable injury to the forest. It is true that their numbers fluctuate from season to season and from year to year, but the elements of the environment are so balanced that they permit survival without permitting excessive multiplication. It is only under abnormal or unusual circumstances that insects become epidemic.[1] Thus in the struggle for supremacy between the different forms of life there is a deadlock. Under such conditions,

[1] Although the derivation of the word *epidemic* should limit its use to human populations, it has been used so generally in connection with descrip-

although the forest may be occupied by numerous potential pests, none will occur in sufficiently large numbers to endanger the welfare of the trees. This static condition is known as the state of *biotic balance*. The importance of this equilibrium cannot be overemphasized. It is only under such a balanced state that long-lived organisms are able to exist at all. The life of a tree extends over a period of a hundred years or more; sexual maturity is only attained after many years of growth. Such long-time processes, obviously, presuppose generally equable environmental conditions.

It must not be inferred from this, however, that each element of the environment remains constant or even relatively constant throughout the life of any individual forest tree. Obviously the ecological picture gradually changes for any tree or for any individual small area as the trees pass from infancy to old age. It has already been pointed out that trees of different ages are susceptible to different kinds of insects. Likewise, different kinds of plants and other animals are associated with each age class of trees. Only in an all-aged forest of constant composition in which the trees on reaching maturity, then senility, and finally death would be replaced by others of their own kind could a continuously static relationship of environmental factors be postulated for any individual small area. It is well known that such a condition rarely if ever exists in nature.

Thus, from the standpoint of any individual tree or any small group of trees, we are usually dealing with only a segment of the complete environmental complex, and the elements present gradually change with the development of the trees. But as one factor ceases to operate, another factor takes its place, so that in spite of this shifting of the component parts, an equilibrium between the tree and its environment is continually maintained until the tree or trees finally reach a condition of senility or decadence. When such a condition is reached, it seems perfectly normal that they should be eliminated by insects, fungi, or a combination of both in order to make room for younger and more vigorous individuals.

Only when large areas are considered, with a normal distribution of tree age classes and associated fauna and flora, is the

tions of insect outbreaks on plants and animals that now such usage seems justifiable.

environmental picture complete. Then each component factor is present and operative, although all of them are never operative on any one spot at the same time. Under such conditions, the *biotic balance* assumes a more static aspect.

But even under such conditions, the balance is static only as long as the composition of the forest remains constant. Natural succession, unless checked by silvicultural procedures, results in a shifting of forces as time goes on, until the climax type is reached. But, normally, throughout these changes the equilibrium between the insects and the trees present at any time is maintained.

The factors reacting to produce the balanced condition that normally exists between any insect species and the various elements of its environment may be divided into two opposing groups, which, under balanced conditions, are equal and opposite forces. On the one hand is the ability of the insect to reproduce itself in a given time under ideal conditions, or its biotic potential; on the other hand is a group of factors that limits or checks the insect in its rate of reproduction and prevents it from realizing its potentiality of multiplication or, as we term it, the *environmental resistance.*

Abundance and Environmental Factors.—Thus in order to maintain a balanced condition the force of environmental resistance must be different for insects that differ in their biotic potentials. For instance, if a species produces 100 eggs per female and the sex factor is 0.5, then its biotic potential of 50 must be matched by an environmental resistance of 50 as long as the population remains constant. Similarly, if a species has a biotic potential of 200, then the environmental resistance must be sufficient to destroy 200 individuals, including parents, for each individual of the parent generation. If the forces are not equal it is apparent that the population will either increase or decrease. The difference between the number of individuals in one generation and the next, after the force of environmental resistance has taken its toll, determines the rate at which a species will increase or decrease. Thus the number in each succeeding generation will equal the number of individuals at the beginning of the generation times biotic potential minus environmental resistance. In order to avoid cumbersome repetition in the following discussion, the letters *BP* and *ER* will be

used for the terms *biotic potential* and *environmental resistance*, respectively.

Now if it is assumed that for any one species the population is to remain relatively constant from year to year, as would be the case under conditions of biotic balance, let us see what must happen if changes are to take place in the environment. Since *BP*—as shown in Chap. III—is a constant for any species, it follows that whenever a change occurs in one set of factors in *ER*, it would have to be offset by comparable changes in other factors of *ER*, or else the population density would not remain constant. For example, if an increase occurred in the available food supply of an insect, there would have to be corresponding compensating changes in some of the other factors of *ER* if the population is to remain unchanged.

Occurrences in connection with studies of the jack-pine sawfly made by the author in Minnesota furnish excellent illustrations of this point. These will be discussed later in detail under defoliators but it seems appropriate that they be mentioned briefly here. Due to an increased quantity of jack pine growing in pure stands, food conditions for this insect have, since about 1910, become ideal. This changed condition resulted in a sawfly outbreak about 10 to 12 years later. But, even after this outbreak, food conditions for jack-pine insects remained favorable. Nevertheless, from 1924 to 1929 the numbers of the sawfly remained below that characteristic of outbreak conditions, and remained approximately constant as a result of increased physical and biotic resistance of the environment. For two seasons a combination of unfavorable temperature and a parasitic disease held down the number of these insects, another year heavy storms at a critical time prevented their increase, and in still another season a late frost was the most important agency of resistance.

In the preceding illustration the abundance of a certain species in one locality was kept approximately constant over a period of years. This constant number was maintained in spite of a changed *ER*, because of compensating changes in other factors of *ER*.

Frequently the value of a certain factor of *ER* may vary with the population density of the insect against which it is working. When the population of the insect is at one level such a factor of *ER* may be relatively ineffective, whereas it may be

very effective at another population level. Smith (1935) proposed the term *density-dependent* to describe these factors in contrast to those that he calls *density-independent* factors.

Some density-dependent factors may operate most effectively on high populations and some on relatively low populations. For instance, insect species that are parasitic or predaceous on other insects, and entomogenous disease-causing organisms increase in their efficiency at high host density and decrease in efficiency at low host density. The rate at which this efficiency increases with host density determines the population level at which the parasite and the host will reach equilibrium. Thus a parasite that is able to produce a high rate of mortality in its host at a low host density will, other things being equal, be economically effective, whereas another parasite that increases more slowly in efficiency with increased host density may be relatively ineffective because of the higher host density at which equilibrium would be attained.

Birds like other predators are density-dependent and are most efficient when their insect prey is sufficiently numerous to offer an attractive reward for hunting but is still at a relatively low population level. This is because the multiplication of birds is limited by their seasonal and spatial requirements so that they cannot increase their numbers materially to take advantage of a food that happens to be seasonally abundant.

The results of this may be illustrated by a hypothetical case. If within the feeding area of an insectivorous bird there are 1,000 insects, each capable of producing 50 young, then the bird will prevent any increase if it eats 49,000 insects, assuming that the adult insects die of natural causes after the breeding period. If the bird's nutritional requirements are satisfied with this number of insects, and instead of 1,000 insects there are 1,000,000, then in a single generation the insects, other things being equal, will increase from 1,000,000 to 49,951,000. Therefore, at one population level the bird would hold the insects at constant numbers, whereas at a higher level it would exercise an insignificant effect. Insectivorous mammals like shrews, skunks, and voles operate similarly. Although they may eat more individuals when their prey is numerous, their own population is relatively so limited that they are unable to exercise much influence when the insects are very abundant.

At different population levels of a certain insect their effects would be as follows: At low levels the insects would not afford a satisfactory reward for hunting, and they would be taken only casually by birds and mammals. At a higher population level the insect would reward the hunter sufficiently to encourage special attention, and predator resistance would increase in direct proportion to the population, until the maximum resistance would prevail at a point where the nutritional requirements of the predatory species were satisfied. Above this point the effect of vertebrate predator resistance would diminish with increased population of the insect.

From this it is evident that predatory animals unable to increase their populations beyond a certain density, because of spatial or seasonal limitations, are most valuable in preventing incipient outbreaks and in lowering the position of population equilibrium below the point at which it would otherwise be reached. On the other hand they are relatively ineffective in checking outbreaks once their prey has attained excessive numbers.

Like the biotic factors of *ER*, the nutritional factors are also density-dependent. When the insect population is low, food for them is adequate and the hazards associated with the search for food are low. These hazards increase with higher population levels, even though the total quantity of food may still be adequate to satisfy the needs of the species. With still higher populations competition for food will result in the maximum nutritional *ER*.

Physical factors are generally density-independent. They act upon the insects regardless of population density. Therefore their chief effect is to determine whether or not an insect can persist in an environment. Cook (1929) has analyzed the effect of physical factors on insects and divides the range of a species into several concentric zones. In the most favorable portion of the range lies the *zone of normal abundance*, within which physical conditions are invariably favorable for the species, and within which outbreaks are controlled or prevented by the action of nutritional and biotic *ER*.

Outside this zone lies the *zone of occasional abundance*, in which the physical conditions are always sufficiently favorable to permit the species to survive, but only occasional favorable variations

will permit them to become excessively abundant. Within such areas, continually favorable niches (Elton, 1927) occur in which the insects maintain themselves as they would in the zone of normal abundance. From these niches they spread when favorable variations permit. In this zone the abundance of the insects is regulated in the niches by biotic factors and in the usually unfavorable part of the zone by a return to usual conditions.

Next comes the *zone of possible abundance* in which conditions are usually so unfavorable that the insect cannot maintain itself except when favorable variations permit invasion from more favorable places. Here the numbers are limited by physical factors when they return to normal.

Another zone might well be added, called the *zone of possible occurrence*, within which physical conditions are never sufficiently favorable to permit the insect to become numerous but within which it might occasionally be found in favorable niches.

From this it would appear that the physical factors are especially important in determining the distribution of a species either permitting it to or preventing it from occupying a given place, but their effect on population level, assuming conditions to be sufficiently favorable to permit existence of the species, is more apparent than real. The success or failure of a species outside the zone of normal abundance depends on the distribution and size of the favorable niches; the physical *ER* being inversely proportional to the area occupied by favorable niches. It is also apparent that an insect is not likely to be economically important throughout its entire range.

If the abundance of an insect species in one locality were contrasted with the numbers of a species having a similar *BP* in a distant locality, we should find that the same underlying relationship existed between abundance and environment. That is to say, if in one locality one set of factors was of higher value than in another region, then some other factors would have to be correspondingly lower if the abundance of the two insects was approximately the same. This is illustrated by a comparison of the factors of *ER* in tropical and temperate regions. In some of the tropical islands, for example, Hawaii, the combined physical and nutritional factors of environmental resistance are of low value. Temperature conditions are particularly favorable and

at the same time food is available the year around; consequently the insects are not compelled to tide themselves over long periods of adverse conditions. In such a climate, biotic factors are much more important and effective than in temperate regions where insects, owing to extreme fluctuations of temperature and periodic scarcity of food, meet a much higher physical and nutritional resistance.

From this discussion it is apparent that the factors constituting *ER* may vary from time to time and from place to place both quantitatively and qualitatively, but that under balanced conditions the combined effects must on the average equal *BP*. It is also evident that when all the factors of *ER* are taken together their effectiveness should increase with the density of the population on which they are acting, if incipient outbreaks are to be checked before they reach dangerous proportions, and that they should also be sufficiently effective at low population levels so that biotic balance may be attained at a level where the insect pests are too few in number to cause economic damage.

A Broken Balance.—If at any time there occurs a change in any set of factors of *ER* without a corresponding change in another set, then the sum total of *ER* will be changed with the result that the population no longer remains constant and the normal balanced condition in the forest temporarily ceases to exist. For instance, if the sum total of *ER* is raised, then the sum total of insect abundance will be lowered. Were *ER* to be raised and continued sufficiently high, the result would be the complete extermination of the insect. We have many extinct species of insects that bear witness to the operation of this force.

On the other hand, if the sum total of *ER* is lowered considerably, then insect abundance may be increased to a point where great damage is done to the forest, and an insect outbreak may be said to exist. For instance, some of the factors that have held a certain insect in check may be so modified that their adverse effect is reduced. Then that particular species, relieved of the pressure that has held it down, becomes very active, gains the supremacy, and dominates its environment.

A specific example of this is to be found in what probably took place in the present-day balsam-fir areas of the Northeast, where the spruce budworm became epidemic. The chief factor that formerly kept this insect in check was the relatively unfavor-

able composition of the forest. This limiting factor was gradually eliminated as the original stands of pine, spruce, and fir were replaced by a climax type of nearly pure stands of fir and spruce through the logging off of the more valuable pine or through natural forest succession. As a result the hazards involved in the search for food were reduced and the numbers of the budworm increased. Eventually one or more other factors of environmental resistance were also changed so that they no longer acted with the same force in holding the insect in check. This may have been due to either a decrease in predators or the occurrence of weather conditions more favorable to insect development, or possibly to both. There are no records to prove just what changes actually took place but it is known that through a combination of circumstances the sum total of *ER* was reduced. The result was that the spruce budworm came to dominate its environment with tremendously injurious effects.

It is possible for adverse weather conditions to disturb the biotic balance not only in the locality where they occur but in localities far removed therefrom. For instance, unseasonable freezing weather in the spring of the year may result in the starvation of insectivorous birds during their migration, with a consequent reduction in the number of these predators in the regions where they nest. This lowering of environmental resistance might conceivably result in an outbreak of a pest in the nesting region.

A Restored Balance.—Whenever the balance is broken, nature ultimately brings about a new balance. In the case of the spruce budworm, mentioned above, the insect increased in numbers until it finally reached a point where there was an insufficient amount of food to bring the larvae to maturity. As a result almost all the insects starved to death; this ended the outbreak. The balsam fir and spruce that survived together with other species have formed a new forest in which spruce and fir, for a time, will occupy a less prominent place. For this reason, the new forest will be a much more stable one than the climax type, and the budworm will occupy a relatively subordinate place therein, at least until the next generation of balsam fir reaches a dominant position in the stand. Thus a new balance has been brought about by nature but at the expense of a tremendous number of trees.

It is to the advantage of man to see that whenever the biotic balance is broken it be restored as soon as possible in order to avoid economic losses. It is even better, when possible to prevent any material disturbance of the original balance. Man's part in maintaining the equilibrium will be taken up under Methods of Control and Silvicultural Practices.

PROTECTION AGAINST ENVIRONMENTAL RESISTANCE

Most insect species are provided with means of overcoming the effects of *ER* when it becomes excessive and thus are able to maintain their population under temporarily adverse circumstances. These same devices result also in raising the average level above the point at which the population would otherwise reach an equilibrium. The effect of these protective forces varies inversely with *ER*. Under optimum conditions, their value is theoretically zero, and each reaches the maximum when the particular factor of *ER* against which it is operative is at its peak. This protective force has been referred to by Chapman as *survival potential*, a term that has caused confusion and therefore will not be used here. The protective factors will be discussed individually in the following sections.

Insurance of Mating.—It has previously been pointed out in our discussion of biotic potential that the sexual type of reproduction is most commonly found among insects and that mating of the two sexes therefore is necessary to the survival of most species. It has also been shown that insects that reproduce sexually have a lower biotic potential than parthenogenetic species. So that in order for the former to keep on any equality with the latter, they require means to overcome the environmental resistance. Moreover, the very necessity for mating, demanding as it does the close proximity of the two sexes, means that the physical factor of space may result in raising the value of environmental resistance for a bisexual species to a higher value than would be the case with the same conditions of environment acting upon a parthenogenetic species. Consequently, insects reproducing sexually have need of something to offset their relatively low values for biotic potential and high values for environmental resistance.

This they accomplish by means of a number of modifications and adaptations for bringing the sexes together. Many moths

are attracted to the opposite sex by odors given off by one sex or the other. A glandular structure on the back of the male tree-cricket provides a delectable feast for the female and by its odor attracts her to the male. Stridulation among the Orthoptera and other orders is frequently a means of attracting the opposite sex, and experiments have shown that the flashing of fireflies serves

FIG. 30.—A walking stick, *Diapheromera femorata*, resting on an oak leaf. These insects use no care in selecting a location for their eggs, but drop them wherever they chance to be at the time of oviposition. (*University of Minnesota.*)

to aid the male in locating the female. All these adaptations tend to insure mating with its consequent reproduction of the species.

Care of the Young.—Even after mating, insects continue their fight against the forces of the environment. They have developed a number of devices for the protection of their eggs and young by which they offset to a certain extent the destructive forces of environmental resistance. Care of the eggs or young by the adults is one of the means by which this is accomplished. Care of the young is usually associated with the higher animals, but nevertheless it manifests itself in primitive ways among some

insects. The highest development of this protection function in insects is usually to be found among the social forms, particularly among the Hymenoptra and the Isoptera, but even among the solitary species it is sometimes strikingly developed, the solitary bees for example.

When an adult insect selects and deposits eggs on the host tree upon which the larvae naturally feed, she is showing a primitive type of care for the young. A rather low degree of care for the young is illustrated by Chrysobothris and other buprestids, which deposit their eggs in cracks in the bark of trees or logs of the tree species upon which the larvae feed. In such places, the eggs are inconspicuous and unlikely to be disturbed before they hatch. To this degree, parental care is found in most insect species, although there are some insects, like the walking sticks, which drop their eggs without regard to location (Fig. 30). Such careless species must, of necessity, have a very high biotic potential if they are to survive, because many of their young will starve before finding suitable food. Such insects are very seldom serious pests.

Fig. 31.—Egg mass of the gypsy moth, *Porthetria dispar*. The individual eggs are hidden by the protective covering. (*Entomological Branch, Can. Dept. Agr.*)

Many moths, such as the tussock moths, the gypsy moth, the tent caterpillars, and others, cover their eggs with a protective material. In some cases this protects the eggs only from excessive evaporation but in other instances, particularly where hairs are included in the covering, as is the case with the gypsy moth, it helps to make the eggs unattractive to birds that might otherwise prey upon them (Fig. 31).

One effective device for protecting the welfare of the young is illustrated by some of the Diptera that are larviparous. These insects hold their eggs within their bodies until after hatching and deposit larvae instead of eggs upon their host. This is true of some of the Tachinidae, many of which are parasitic upon the

larvae of forest insects. The young of larviparous species have a much better chance of gaining entrance into an active host than do the oviparous flies, because as larvae they penetrate quickly into the host and are much less likely either to be rubbed or molted off than if they were required to spend some time in the egg stage on the surface of the host's body.

Protection by the adult of the larvae or nymphs beyond the selection of the proper food is rather rare among forest insects with the exception of the social species. In most instances, the larva, having been placed near a supply of food, must shift for itself. The mother aphid and the mother tingitid are usually found near their young and are sometimes said to guard their young, but it is open to question whether or not this proximity is an example of parental care. More likely it is a question of convenience. In the social species, however, occur many striking instances of a most meticulous care for all the immature stages. It is not the mother but definitely designated workers in these social species that usually care for the young. The mother, or queen, as she is usually called, attends strictly to oviposition. The young of both termites and carpenter ants are cared for in this manner. The workers not only feed the young but in the case of the carpenter ant they carry the young from place to place in the nest in an attempt to keep them under as favorable conditions as possible.

Defense.—From the foregoing, it is evident that a primitive type of care for the young is common among forest insects. It is also apparent that the degree in which it occurs is not sufficient protection to insure the survival of the species. Insects, therefore, must be provided with other means of protection.

Some species have, either in the immature or adult stages or in both, disagreeable odors or flavors making them distasteful to predaceous animals that might otherwise feed upon them, and this serves them as a means of defense. The Pentotomidae and other plant bugs, certain beetles, and some butterflies are notable examples of insects possessing this means of defense.

Many insects are protected by their inconspicuous coloring or form. Few observers of nature have failed to notice how most insects blend into the background on which they rest. Even some of the most gaudily colored species are comparatively inconspicuous in their natural environment. Protective coloring

and protective form are so characteristic of insects as to be obvious to the most casual observer.

There are, in general, two distinct types of protective appearance. In the first type, the color or pattern of the insect's markings blends into its general environmental surroundings. Leaf hoppers, aphids, the carpenter moth, the underwing moths, and many other insects exemplify this protective coloration. In the second type the insect resembles in form and color some part of the plant on which it lives, or in some cases it may resemble some other insect that is either distasteful to or feared by insect predators. This last method of protective resemblance is known as mimicry (Gerould, 1916). There are many well-known examples of insect species that resemble parts of the plants upon which they occur, for instance the tree hoppers,

FIG. 32.—*Chalcophora virginiensis*, one of the buprestid beetles that is protected by its extremely hard exoskeleton.

the walking sticks, and the spanworms. One of our most common examples of mimicry is that of the viceroy butterfly. This insect is an almost perfect mimic of the monarch or milkweed butterfly, which is said to be very distasteful to birds.

In addition to the various means of defense already mentioned, many insects are provided with mechanical contrivances that are of help in protecting them. The hard exoskeleton of the buprestids (Fig. 32) and other beetles makes them much less vulnerable than if their bodies were soft. The sharp spines with which the caterpillars of the brown-tail moth and the tussock moths are armed serve as an effective means of defense against many insect-eating birds. These barbed venomous spines are extremely irritating to the skin of man, and those of the brown-tail larvae, by working their way into the skin, cause irritation called the *brown-tail rash.* This is a common trouble among people who are forced to work where these caterpillars are numerous. Other mechanical means of defense may be mentioned,

for instance, the strong mandibles of many forest insects. These are ready weapons of defense and are frequently used effectively. Another powerful weapon with which some of the Hymenoptera are provided is the venomous sting. By means of the various methods of defense, insects are often able partially, at least, to

FIG. 33.—A nest of the fall webworm within which the larvae are protected from the attack of some enemies. (*University of Minnesota.*)

prevent the normal reduction of their numbers resulting from the action of environmental resistance.

The Use of Shelter.—Some forest insects are able to evade at least partially the force of environmental resistance by retiring into shelters of various sorts. Shelter protects insects to some degree against changes of weather and also makes them less easily found by their enemies. These shelters may be constructed of silk or wax secreted by the insect itself, or of other

materials such as sticks, stones, wood, or earth, or of combinations of some of these materials.

Fig. 34.—Norway-pine needles heavily infested with pine-leaf scale. Each white spot represents a single scale insect covered with its protective shelter. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

One type of insect shelter, with which everyone is more or less familiar, is the cocoon. By means of this structure, the pupa is protected during its period of quiescence. Some insects when in the larval stage build cases of silk and other materials for their protection throughout the developmental period. The bagworms, for instance, carry a case about with them from the time they hatch until they are fully grown. As the larva grows the case is enlarged to accommodate it. The female bagworm never leaves the case but lays her eggs and dies therein.

The spruce budworm and some others of the same group construct another kind of shelter. During the larval period they work under a light web of silk that they spin. The tent caterpillars and the fall webworm build nests of silk into which the larvae retire or within which they feed (Fig. 33). Other species, like the armored scales and the woolly aphids, are sheltered by their own waxy secretions (Fig. 34).

Some species of insects make use of their food material as shelter. Leaf miners are sheltered between the upper and lower cuticula of the leaves in which they feed (Fig. 35). Cynipids, gall aphids (Fig. 36), and gall mites find both food and shelter in the abnormal plant growth

for which they are responsible. The bark- and wood-boring insects are well sheltered in the tunnels and galleries that they cut.

Certain subcortical species, like Rhagium and Pytho, construct pupal cells of frass and chips beneath the bark where they have

FIG. 35.—Blotch mines of Lithocolletis in a burr-oak leaf illustrating how these delicate insects are sheltered between the upper and lower cuticula. (*University of Minnesota.*)

been working, thus forming an effective shelter for the pupae. From these examples it becomes evident that insects have come to make use of many different types of shelter, but all types, whatever their character, aid the insect occupant in overcoming the resistance of its environment.

Locomotion.—When a predaceous insect or a parasite approaches an insect, or when unfavorable temperatures or unsuitable moisture conditions occur, an insect has two choices.

It may remain quiescent, trusting that its enemy will not notice it or that the temperature or moisture conditions will remain within its range of tolerance, or it may try to escape.

Adult insects are, as a rule, well provided with the necessary means of locomotion. Most of them possess both legs and wings that they are able to use effectively. By means of these appen-

FIG. 36.—Galls sheltering one of the poplar gall-aphids of the genus Pemphigus. (*University of Minnesota.*)

dages they are enabled to escape either from their enemies or from locally unfavorable physical conditions of the environment (Chapman, 1925). Furthermore, the ability to move about easily and quickly helps to bring together the sexes, thus insuring successful mating. It also helps the insect in its search for food, often makes possible effective distribution, and helps the insect to place its eggs in locations favorable to the larvae, even though this may necessitate a considerable amount of moving from place to place.

Larvae, on the other hand, are generally much less able to move about from place to place. None of the immature stages

of insects have functional wings with the exception of the may flies which have a subimago winged-stage. Larvae must, therefore, depend primarily upon their legs for their locomotion except as they are carried from place to place by birds, other animals, vehicles, or by wind (Fig. 37). Some of them have well-developed legs and can move about rapidly but many others, the caterpillars and grubs, for instance, can move only slowly from place to place. But even this feeble ability to move makes

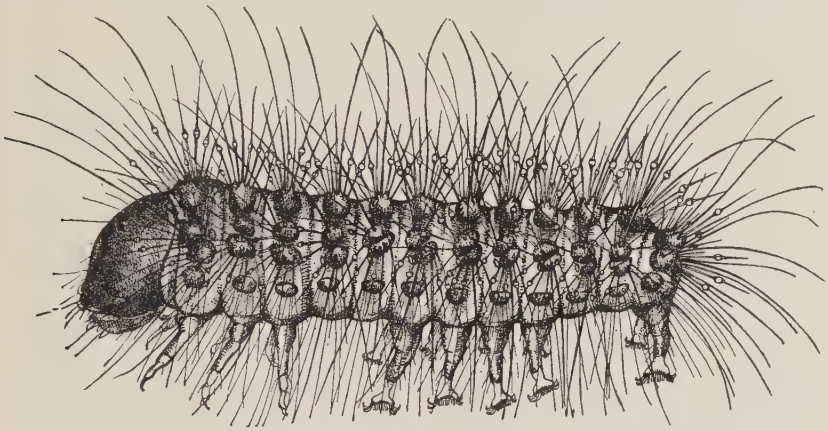


Fig. 37.—First instar larva of the gypsy moth showing long clothing-hairs and the so-called "ballooning" hairs. These hairs so increase the surface of the insect in proportion to its weight that it can be carried long distances by air currents. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

it possible for many of them to gain more favorable conditions of moisture or temperature, or to improve their food conditions. This is true of practically all insects that feed upon the surfaces of plants. The miners and borers, on the other hand, either cannot move at all, or move with exceeding slowness from one place to another and, therefore, with the exception of some like the carpenter-moth larvae, which move back and forth in their galleries, they must take what comes whether it is good or bad. Such insects, as a result, have a much more limited sphere of activity; and they are, therefore, confined to those locations where the extremes of environmental conditions always lie within their zone of toleration. The motile species, because they are better able to adjust themselves to changing conditions, have a much wider range of activity, and when conditions become unfavorable in one place they move to another.

In addition to the use of their legs, many lepidopterous larvae have another means of locomotion that is useful for protection. These larvae are able to spin very rapidly a thread of silk on which they can drop out of the way of harm. A larva, having dropped on its thread, can return again later when it is safe to its original position; or small larvae may parachute for long distances suspended at the end of a free thread. All these means of locomotion are a distinct aid to the insects in overcoming environmental resistance.

Migration and Dissemination.—At some time during the year, almost every species of insect passes through a period of local dissemination in which the individuals move out in various directions in search of suitable new locations. This movement usually takes place in the adult stage, but in some instances it may also occur in the larval stage. As a result of this movement out from centers of concentration, almost every suitable breeding place may receive its share of the moving insects. Sometimes this movement is very limited in distance. For instance, it has been found that the walking stick, *Diapheromera femorata*, because it is wingless and not especially active, moves out from centers of infestation at the rate of only ⅛ mile per year (Graham, 1937), whereas *Dendroctonus brevicomis* apparently may fly for miles from the trees in which it developed.

The efficiency of insect distribution can well be illustrated in any large coniferous forest area that has been killed by fire in the spring of the year. Even though the area of killed trees may be 100 square miles or more, practically every suitable tree will be infested with a share of such borers as Monochamus, Ips, Chrysobothris, certain species of Siricidae, and other subcortical and xylophagous insects. There could not possibly have been present in the area before the fire sufficient adults to reproduce the multitude of borers found in the area after the fire. It is evident, therefore, that they must have flown in from the surrounding territory. The omnipresence of certain leaf eaters in every suitable location is still further proof of the general distribution of at least our common species.

The search for food or for what usually amounts to almost the same thing—a suitable place for oviposition—is the chief cause of dissemination; but, apparently, even when food and places for oviposition are abundant, insects may still move about.

Dissemination is a means by which the intensity of local environmental resistance may be reduced. The value to the species of the ability to move out from centers of concentration is inestimable, because the more widely a species is distributed the less likely it is to be wiped out by some local adversity.

Some insects migrate, within the same general locality, from one host plant to another. Frequently this involves alternation of hosts, which is the transfer from one host species to another and then later a return to the original host. This sort of migration is common among aphids and adelgids. A few, like the monarch butterfly, migrate over long distances in a manner similar to avian migration. Some, like certain coccinellids or ladybird beetles, move from low to high altitudes in late summer and autumn and return to lower elevations in the spring. But usually the movements of insects are relatively local.

Tropic Responses.—Some insects possess other most interesting characteristics that they are able to use to their advantage in the struggle for existence. These abilities relate to the orientation reaction of the insect's body with reference to some physical or chemical effect and are commonly called *tropic responses.* For instance, when one of the hover flies habitually faces into the wind when flying, it is exhibiting a tropic response called *positive anemotropism.* Species that respond positively anemotropically may by the exercise of this response when living near the seacoast prevent themselves from being blown out to sea and thus reduced in numbers.

Examples of other types of tropic responses are numerous. In the autumn the ladybird beetles tend to orient themselves when on a vertical surface in such a way that their heads are directed away from the center of the earth. They are then said to be *negatively geotropic.* Under such conditions, if they move at all, they will of course climb upward on the surface upon which they are resting. These same insects when seeking a place to hibernate are also *positively thigmotropic;* that is, they respond positively to the sense of touch and, by creeping into cracks, so orient their bodies as to bring them into as close contact as possible with surrounding surfaces. Many insects respond either positively or negatively to chemical stimuli and are then said to be either *positively* or *negatively chemotropic.* Insects that turn toward the light are *positively phototropic,* whereas those

that turn away from the light are *negatively phototropic.* Those that seek out sunny places are *positively heliotropic,* whereas those that shun the sun are *negatively heliotropic.*

These terms are descriptive of how insects respond to external stimuli. They do not in any way explain why insects react in certain ways. It must be clearly kept in mind that the terms are descriptive rather than explanatory in order to avoid the common error of trying to explain the cause of certain reactions merely by giving those reactions a name.

Through many generations, natural selection has brought about a survival of those insects which have come to respond in ways that are favorable to the species. Thus it is that tropic responses have had during the course of evolution an important influence in determining how successful an insect will be in overcoming environmental resistance. The insect that orients itself in relation to environmental forces in a way that is most likely to be favorable to it is much more likely to survive than one that is erratic in its reactions or one that fails to react at all. Some authorities think that practically all the activities of insects are the results of tropic responses; even if this is not entirely true it cannot be doubted that tropisms play an exceedingly important part in the life of insects and that they determine to a large degree whether or not an insect will succeed in the environment in which it finds itself.

The Effect of These Protective Forces.—From the foregoing, it is evident that an insect's abundance depends not only upon the biotic potential of the species and the amount of environmental resistance but also upon the inherent ability of each insect species to meet and reduce in various ways the force of environmental resistance. Like other inherent qualities, this ability varies with different species. It also varies with varying conditions. Under optimum conditions, the ability of insects to overcome environmental resistance is not needed and is, therefore, inoperative. But when pressure is increased so that this ability is needed, its operation becomes more and more important until finally under conditions of extreme environmental pressure it may be so important as to determine whether or not a species may survive. Thus, by acting with increasing power as environmental resistance increases and with decreasing power when resistance is reduced, the ability to overcome environmental

resistance tends to stabilize insect numbers and to reduce the extreme fluctuations in abundance that might otherwise occur as the result of fluctuations in the environment. In other words, this stabilizing force operating in all species helps to maintain the biotic balance.

ABUNDANCE AND INSECT INJURY

It has already been indicated that the abundance of an injurious insect determines its economic importance. Excessive numbers, from the economic standpoint, may occur as sporadic outbreaks, as periodic outbreaks, or, because the average population level is above allowable economic limits, thus being continually abundant.

Sporadic Outbreaks.—Most insects that are injurious to the forest fall into one of the first two groups. Sporadic outbreaks are usually associated with changed conditions, often the result of man's activities. These changes are usually temporary in character and result in a brief flare-up of an insect population followed by a return to normal. Good illustrations of this type of outbreak are the bark-beetle infestations so common about new log structures built in coniferous forests, the spot infestations along newly opened highways, or similar infestations about decks of freshly cut logs. The insects remain abundant while attractive conditions prevail, and the population returns to normal when these conditions cease to exist. If, however, environmental conditions fail to return to normal, a new and injurious average population level may be established. This seems to have happened in the case of the bronze birch-borer in the Lake states (Hall, 1933) and the two-lined borer in parts of Minnesota.

Periodic Outbreaks.—Periodic outbreaks are characteristic of many defoliators that become injuriously abundant at more or less regular intervals like the spruce budworm, the pine and fir tussock-moths, the pandora moth, and numerous others. These periodic outbreaks are population oscillations of high amplitude that follow the life history of the forest, or perhaps weather or biotic fluctuations. They are often determined by the period required for the forest to recover and develop to a susceptible stage following a previous outbreak. These periodic outbreaks are usually catastrophic in character, and usually result in the death of a considerable part of the attacked forest. They

constitute some of the most important forest-insect problems. Their control, as will be shown later, depends on man's ability to maintain conditions in the forest that are, in general, unfavorable to large populations of harmful insects.

Continual Abundance.—Insects that normally maintain an average population level above allowable economic limits are not common in the forest. In this respect, forest entomology differs from horticultural entomology, where concentrated annual products in the form of fruits may be completely ruined for market by an infestation of insects like the fruit maggots or the codling moth that actually injures the tree only slightly or not at all.

Also in agriculture and horticulture, in contrast to forestry, crops are grown for obvious reasons under unnatural conditions in pure stands. Such conditions tend to reduce *ER* for the pests of these crops, with the result that the population level is likely to be higher than otherwise would prevail. In the forest, unnatural conditions are often the cause behind abnormally high population levels of insects. For instance, logging and fires have resulted in the development of pure oak forests in central Michigan, in which walking sticks are unusually abundant (Graham, 1937). Also, the present excessive abundance of open jack-pine stands in the Lake states is accompanied by excessive populations of the spruce budworm, the hemlock scale, and other pine insects. As a general rule the insects that are characterized by continuous excessive abundance are not those that attack living trees but are chiefly those that attack logs, lumber, wooden structures, furniture, and other wood products, where even slight damage may result in serious loss.

The selection of control procedures to be used against forest insects will depend in part upon these population characteristics. Means of preventing the development of excessive populations, whether they are sporadic, periodic, or continually abundant, will be considered in the following chapters.

CHAPTER VI

DIRECT CONTROL OF TREE INSECTS

Insect control may be defined as the regulation of insect activities in the interests of man.

The Purpose of Control.—The success of control operations is measured by the degree to which the product or crop protected escapes serious injury by insects. It is generally recognized that it is practically impossible to exterminate any forest pest, and, even though practicable, extermination might not be advisable because it might easily result in allowing an even more serious pest to occupy the niche vacated by the species destroyed. The aim of forest-insect control is not extermination, therefore, but is to keep the pests within reasonable bounds. It has been shown that outbreaks of forest insects occur as the result of a disturbance of the biotic balance, and that as long as the balance can be maintained outbreaks are impossible. In its simplest terms, the purpose of control is to maintain a balance between pests and hosts at such a level that economically important injury will not occur.

Of all the influences disturbing the balance, the activities of man are the most far reaching and important. The cutting of trees, the building of trails and roads, the construction of buildings, the drainage of land, the damming up of water; all these and in fact practically all man's activities tend to modify or change environmental conditions and thereby to increase or decrease the probability of insect outbreaks.

Inasmuch as the value of the forest to man depends upon the use he can make of it, it is obvious that it is neither possible nor desirable to attempt to eliminate man's activities in the forest. Effort should be made, however, to carry on these activities in such a way as to disturb the balance as little as possible. Furthermore it should be kept in mind that in order to preserve a safe condition in the forest, whenever man, in the course of his activities, removes or reduces the effect of any factor, or factors, he

must substitute another force of equal value. This is what we do when we carry on control measures. We are merely substituting one set of limiting factors for another set that has been removed.

Good illustrations of this point are common in agriculture. For instance, the Colorado potato-beetle originally was kept in check under natural conditions by food limitations. The individual plants of the native species of Solanum upon which it fed were scattered, and consequently the difficulties and dangers attendant upon finding food were great. As a result, enough beetles were lost so that the number per unit area remained low and approximately stationary from year to year, thereby producing a balanced condition between the beetle and its host. When potatoes came to be cultivated as a field crop in the natural range of the beetle, food became so abundant that it ceased to be a limiting factor. Under the new conditions the beetles that drifted into potato fields found there that almost any plant upon which they chanced to alight provided suitable food and that the risks connected with hunting for food were much reduced. When the beetle, therefore, became established in cultivated fields, this formerly innocuous species promptly became an important pest not only in its native haunts, but also over wide areas where it was not native. It was obviously impossible to grow potatoes in a mixed stand and restore the conditions of food limitation that originally existed, therefore it was necessary to introduce some other limiting factor. The potato plants are now sprayed or dusted with some arsenical to poison the beetle; and as a result a new balance, which is even more favorable to the potato than the condition existing in nature, has been established.

The Cost of Control.—Like every other forest operation, the application of forest-insect control must be looked upon from the business point of view. It must always be kept in mind that the material saved by the application of control measures must justify the expense involved. The cost of control must be materially less than the loss that would have occurred had no protective measures been applied. The lower the value of the trees or wood products to be protected or the smaller the margin of profit, the smaller will be the amount that can justifiably be expended for protection.

With this in mind, the conditions that face the forest entomologist will be considered. As a rule the nearer the ultimate prod-

uct is approached, the more valuable the materials become. In the early years of the forest rotation, the value of the trees is comparatively small. At that time, even small injudicious expenditures may easily wipe out the entire expected profit. The value of mature timber justifies greater expenditure for its protection

FIG. 38.—Spraying lodgepole pine in Yellowstone Park for the control of defoliating insects. The value of a timber forest would not justify such expensive operations as this. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

than does the value of younger trees; the value of partially manufactured products justifies a greater expenditure than does standing timber; and in the protection of manufactured wood-products a still greater expenditure is justified.

Trees may have very real values in checking soil erosion, or for esthetic purposes. These indirect values must be taken into consideration along with commercial values in planning for their protection. Where trees are used to prevent the erosion of soil on steep slopes and watersheds, their destruction means not only the loss of a certain amount of wood but also damage through erosion of hillsides and silting of reservoirs. Such damage, by comparison with the loss in wood, may appear infinitesimal.

Under such conditions, larger expenditures for protection than in the timber forests are justifiable. Likewise, park and shade trees have an esthetic value far in excess of their value for wood. This value is estimated by some of our best landscape architects and tree surgeons to be $5 per circumferential inch for well-placed perfect trees of the best species. Commensurate appropriations for the protection of such trees may be made economically (Fig. 38).

Thus, the control measure that can effectively and profitably be used against an insect attacking shade trees may be impractical in the forest because of the excessive expense involved. The control measure must, therefore, be suited to the conditions under which it is to be applied, and under each different condition we may be forced to use a different method of control even for the same insect.

On the basis of justifiable cost of control, forest insects may be divided into three major divisions: (1) forest pests, (2) shade-tree pests, (3) forest-products pests. Many of the same insects may be active in each division, but the methods of control will be quite different. The conditions under which they are working in each case will determine the appropriate methods of control. The real problem of the forest entomologist is to develop not only ways by which insect ravages may be checked but also methods that can be applied economically under specific conditions. He must continually bear in mind that the control measure he recommends must show a profit from the operation if it is to be justifiable.

In this discussion of the control of tree insects, various methods will be considered, and the general conditions under which each can be made applicable will be pointed out.

The Classification of Control Measures.—Methods that can be used for the control of tree insects may be classified into more or less arbitrary groups as follows:

A. *Direct Control.*—Operations aimed directly at the insect for the purpose of immediate suppression.
   1. Mechanical methods:
      Collecting, trapping, destroying infested materials, barking to destroy broods, heating.
   2. Biotic methods:
      Predators and parasites used for immediate suppression.

3. Chemical methods:
   Dusting, spraying, fumigating, using poisonous bait.

B. Indirect Control.—Operations designed to modify environmental factors to secure ultimate limitation of insect numbers.

1. Chemical and mechanical methods:
   Modifications of food supply, moisture conditions, and temperature conditions.
2. Biotic methods:
   Competition, introduction or encouragement of parasites and predators.
3. Silvicultural practices:
   Regulation of composition and density, selection of site, regulation of drainage, selection of resistant varieties and species.
4. Statutory regulations:
   Quarantines, embargoes, inspection, and certification.

DIRECT CONTROL BY MECHANICAL METHODS

As the science of economic entomology has developed, many means have been devised for the control of insect pests in general (Wardle and Buckle, 1923). Until very recently most of these have been direct methods, and some of them are applicable to the control of tree insects. Many of these direct methods of control have had their origin in Europe, but others, spraying, for example, have been originated and developed to their present high degree of efficiency in America. Wherever they are used, direct methods are generally of a curative nature.

Collecting Insects.—One of the most obvious methods of insect control is the direct attack upon the pest by collecting and destroying it during some one of its stages. Such methods are, of course, expensive and can be used only under particularly favorable circumstances. Numerous instances where insect outbreaks have been held in check by these means could be cited, however, particularly in Europe. Also, in some of our American cities, shade-tree pests have been controlled in this way; for instance, in Minneapolis an incipient outbreak of the white-marked tussock-moth was checked through the cooperation of Boy Scouts and other school children with the civic authorities in collecting and destroying the egg masses of this defoliator.

One of the methods frequently recommended for controlling the white-pine weevil is by collecting the adult weevils in the early spring during the feeding period that precedes the period of oviposition. The beetles are knocked off the pines into a net

by jarring the terminal shoots. Such a method may be practicable on ornamental trees but it too expensive to use in forest plantations.

Trapping Insects.—Many ingenious devises for trapping insects have been developed by entomologists, chiefly pits or furrows, light traps, bait traps, trap logs, and trap bands. The use of trap pits or furrows is commonly recommended in European literature for the capture of insects that spend at least part of their active life on the ground, but owing to the excessive labor cost it has seldom, if ever, been used in American forests. Trapping by means of lights has been used to some extent in this country, but unfortunately it has not proved very successful, because the insects attracted to lights are largely males, and the few females that are caught by these devices have in many cases already deposited their eggs. Gravid females are seldom attracted in large numbers to ordinary lights. Recent experimental work indicates that trapping results with lights may, in some instances, be improved by using colored lights. Some insects are attracted by one color and some by another. Traps baited with some attractive food material or chemical have been somewhat more successful in capturing females. Such traps have been used especially in experimental work, with such insects as the oriental fruit moth, the gypsy moth, calosoma beetles, and the Japanese beetle as indicators of population density. Fermented sugar or molasses baits are attractive to many insects, but rapid advances are being made in developing baits that are more or less specific for certain insects. For instance, geraniol is especially attractive to the Japanese beetle, and traps baited with this chemical are used to indicate the presence or absence of the beetle in a locality. Further developments in methods of trapping adult insects before they have laid their eggs may provide foresters with an effective means of insect control.

In European forests, trap logs and trap trees intended to protect standing timber from the attack of bark beetles are sometimes used. The principle involved is that certain species of these beetles prefer freshly cut or girdled trees to healthy uninjured trees; as a result, they will deposit their eggs in freshly cut logs or girdled trees provided by the forester for this purpose. Later the broods of beetles in these traps can be destroyed. This method has not been much used in America, but it is quite

possible that it may eventually find a place in our ultimate plan of insect control.

In the control of certain of our shade-tree pests that tend to congregate in secluded places during some portion of the day, the gypsy moth for instance, loose bands of burlap or other

FIG. 39.—Burlap band on an oak tree. Gypsy-moth larvae have congregated beneath the band where they can easily be killed. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

material placed around the tree trunks are sometimes used. The insects will gather under the protection of the band and can easily be destroyed there in large numbers (Fig. 39). This method is, of course, applicable only to shade trees.

Destroying Infested Materials.—In forest entomological literature one of the most frequent recommendations for the control of bark beetles and wood borers is to cut and burn the infested

portion of the tree. Doubtless this is an effective means of control provided that practically all the infested trees in a community are treated in this way. Consequently, cutting and destroying the infested portion of trees become a community control method. One insect that might be controlled by this

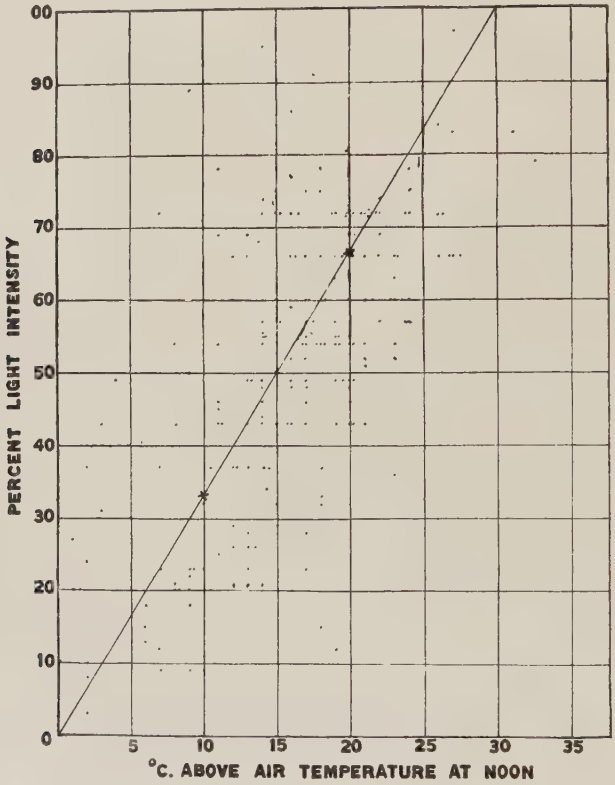


Fig. 40.—Graph illustrating the relation between subcortical temperature and light intensity. Each dot represents a daily observation.

method is the two-lined borer. If by community cooperation all dying trees were cut before the beetles emerged an outbreak of this insect could be checked. This method is, however, primarily of use in protecting shade trees and forest products and will always have a limited application under forest conditions.

Barking to Destroy Broods.—In certain cases, notably in the control of dendroctonus beetles, the barking of cut or standing trees has been employed to destroy broods of these injurious

insects. Some of these beetles spend their entire life in the phloem region between the bark and wood, while others spend a part of their life in the corky layers of the bark. Where the latter type is concerned, the removed bark should be burned or exposed to the direct rays of the sun in order to destroy the insects in the bark. Such operations are designed to reduce the number of beetles to the point where they cease to be a menace to the surviving trees.

The Application of Heat.—The use of heat to kill wood-boring insects is a comparatively recent development. It has been shown that the temperature beneath the bark of logs lying in full sunlight frequently exceeds the fatal temperature of log-inhabiting insects. The amount by which the temperature beneath the bark on the upper side of such logs exceeds the temperature of the surrounding air is, other factors being equal, directly proportional to light intensity (Graham, 1920) (Fig. 40). By turning logs every week or two during warm, bright weather it is possible to destroy all insect life in the surface layers of the logs (Craighead, 1920). It was this principle that was applied in the preceding paragraph to destroy bark-beetle broods in the bark removed from infested trees. For the successful killing of insects it is essential that the material to be treated be exposed to the full force of the sun's rays.

In the process of kiln drying, temperatures in excess of the fatal temperature of wood-boring insects are almost always obtained. Even the lowest kiln-seasoning schedule with temperature ranging from 105 to 115°F. has proved effective in killing certain species (Craighead, 1921). The higher schedules appear to be effective for all wood-inhabiting insects.

DIRECT CONTROL BY BIOTIC METHODS

Although biotic factors in insect control are usually used indirectly, there are some instances where their use is aimed directly at a certain species of insect for the purpose of its immediate suppression. When biotic factors are employed for this purpose, they are being used as direct means of control. Numerous attempts to apply biotic methods in this way have been made, but most of them have never passed beyond the experimental stage. In a few instances, however, these efforts

have been attended with more or less success. Some of the successful efforts have been so striking in their results that it is possible we may see a much wider application of this kind of control in the future.

Illustrations.—The most striking example of the successful direct application of biotic methods to the control of an insect pest is to be found in California. In the citrus orchards of that state, the mealybug, *Pseudococcus gahani*, has been a most serious pest. From 1918 to 1929 it was effectively controlled by the direct use of a predatory beetle, a coccinellid called *Cryptolaemus montrouzieri*. According to Smith (1925–1926–1932), the use of this method passed beyond the experimental stage and proved itself to be not only effective but also much cheaper than chemical or mechanical methods of control.

The procedure followed has been to rear these predaceous beetles in large numbers and liberate them in the infested orchards in sufficient quantities to destroy the mealybugs before they have caused much damage. Special insectaries for the rearing of the beetles are operated in strategic locations on the proceeds of the sale of the beetles reared. During the season of 1929, over fourteen million beetles were produced by these laboratories and as a result the mealybugs were effectively controlled over an orchard area of about 75,000 acres. The total cost of this work was approximately $125,000. The beetles were not liberated in every orchard in the infested region but were concentrated in those that were in danger of serious injury. If it is assumed, as Smith does, that one-third of the orchards were actually treated, the cost per treated acre was about $5.00. If, however, the cost is spread over the entire 75,000 acres affected, the cost per acre was only $1.66. When compared to spraying, which costs in the neighborhood of from $25 to $30 per acre for one application, the expense of this method of control is exceedingly low.

At present, Cryptolaemus is not being used so extensively as formerly, because the citrophilus mealybug has been brought under excellent indirect control by the introduction of two very effective internal parasites, *Coccophagus gurneyi* and *Tetracnemus pretiosus*, introduced from Australia in 1928. The use of cryptolaemus is now mostly limited to the control of another somewhat less injurious mealybug. Nevertheless it still remains

one of the most striking illustrations of how a predatory species may be used directly for the control of a noxious species.

Attempts have been made to rear and utilize parasitic insects in the same way. *Trichogramma minutum*, a tiny egg parasite, has been the subject of much unsuccessful experimentation. At present the Canadian Parasite Laboratory is having some success in rearing and distributing parasites of certain pests for the direct control of these insects in greenhouses. But thus far there are no illustrations of the practical use of parasitic insects for the direct control of tree pests. Neither have we an authentic case of the successful use of fungi, bacteria, or other parasitic forms to bring about immediate suppression of a forest insect. One attempt to control a forest pest, the larch sawfly, was made by Hewitt in Canada, who tried to distribute an entomogenous fungus in forests that were being injured by this insect. Unfortunately, the attempt was a failure.

There is, however, one instance where a fungous disease was used with apparently successful results against an agricultural pest. In the Central states such a disease-causing organism was distributed for the purpose of checking a chinch-bug outbreak and was followed by the destruction of the bugs. It is, however, the consensus of opinion that this may easily have been a coincidence. The spread of the disease was apparently made possible by favorable weather conditions. Inasmuch as the disease organism was already present to some extent in the region, the favorable weather that occurred might have been sufficient in itself without the distribution of the inoculum by man to make possible the epidemic that destroyed most of the chinch bugs.

Obstacles.—The success of fungous and bacterial diseases in reducing insect abundance depends so much upon favorable weather conditions that the use of these organisms offers comparatively little promise. Other organisms not so dependent upon the weather may ultimately be used directly, but at present so little is known about insect diseases that little hope can be held out for their immediate use.

The successful use of insect parasites and also of insect predators depends upon the possibility of rearing them on a large scale at a reasonable cost. If it were not for difficulties in the technique of rearing these organisms we should now be able to use them extensively in direct control.

One of the greatest obstacles to be overcome is the difficulty of providing a sufficient quantity of suitable food to make wholesale rearing possible. This is no easy task. It necessitates either the rearing of large numbers of hosts to furnish food for the parasites or predators that are produced, or the development of some satisfactory artificial food. The latter feat has so far never been accomplished, although it holds distinct possibilities.

In the rearing of the predaceous beetle, Cryptolaemus, in California, the food problem has been solved in a very ingenious way. It was found that mealybugs can be produced in large numbers by feeding them upon potato sprouts. By making use of this cheap and easily handled food for producing adequate quantities of the beetle's prey, this predator can be reared at a comparatively small cost. It is easy to see that if it were necessary to rear the mealybugs on citrus trees in order to provide food for the predators the rearing of the latter would be so expensive as to be prohibitive. Struble (1938) in an unpublished report describes the successful use of fly larvae as a food for certain predatory beetles that attack bark beetles. He is now conducting experiments in the mass rearing of some of these beneficial insects.

Although none of them presents so great a difficulty as the provision of suitable food, other obstacles in the way of large quantity production of parasites or predators also exist. For instance, it may be difficult to obtain mating (Jones, 1926), or transportation of the insects to the localties where they are needed may present difficulties. The problem of synchronizing laboratory production of parasites with the development of the pest in the forest so that a maximum supply of the beneficial species will be on hand at the proper time must be solved. Until these obstacles are overcome we shall be forced to turn in most cases to other kinds of methods for the direct control of forest pests, and to leave the use of biotic factors to the more indirect phases of control work.

CHAPTER VII

DIRECT CONTROL BY CHEMICAL METHODS

In the foregoing chapter it was shown that, with a few exceptions, biotic methods of direct control are not yet developed to a point where they can generally be applied, but that mechanical methods are being used in a number of instances where the cost is not prohibitive. We are now ready to consider the most generally used methods of direct-control work, namely, chemical methods.

FEASIBILITY OF CHEMICAL METHODS

The use of chemicals for the control of insects has had a phenomenal development since 1868, when paris green was first used against the colorado potato-beetle. Since that time insecticides have been improved and perfected to such a degree that chemical warfare against insects has come to be almost universal. Until recently, its use in the control of tree insects has been limited to shade and orchard trees. Because of the high costs involved in applying insecticides, and because of the inaccessibility of forest lands, this method has in the past found very little use in forests.

The Questions of Cost and Machinery.—Recently, however, the development of poison dusts and of methods for applying these dusts, particularly the use of airplanes and autogiros, has opened up a new field of possibilities in the chemical control of forest defoliators (Fracker and Granovsky, 1928). By using air machines equipped with a suitable apparatus for distributing the dust or spray it is possible to apply insecticides on forests that would be absolutely inaccessible to any ground machine (Fig. 41). The cost of dusting in this way, which usually exceeds $5 per acre, is not excessive in cases where very valuable timber is being protected. It is too high a cost, however, for use under ordinary forest conditions. Furthermore, if this method of control were generally practiced on forests, the areas to be covered would, at

certain times, be so great that the available supply of arsenicals would be insufficient to meet the demand. This method of control, therefore, will, in all probability, always be confined to comparatively small areas of valuable timber and to the control of spot infestation which, it is feared, may spread and involve extensive forest areas if allowed to go unchecked.

The high-powered liquid sprayer of large capacity has accomplished excellent results in the control of such defoliators as the gypsy moth, when applied to valuable trees in parks, on lawns,

FIG. 41.—Dusting a forest by the use of an airplane to control the hemlock looper, in Peninsula State Park, Wisconsin. (*A. A. Granovsky.*)

and near roads (Kotinsky, 1921). By means of a special nozzle, the spray can be thrown to the top of tall trees (Figs. 42, 43), and by means of long leads of hose, it is possible to work back from the roads for several thousand feet. The cost of spraying is, however, much too high to warrant the use of this method of insect control in the timber forest. It is, nevertheless, and probably always will be, an important method of fighting park- and shade-tree pests. High-powered spraying machinery should be a part of the equipment of every well-organized municipal tree department.

The Effect of Poisons.—But aside from the cost and mechanical feasibility there is another angle to chemical control that should not be overlooked. Even though the economical application of poison to extensive areas proves a practical possibility, little is known of the effect that the extensive application of a poison would have upon forest life in general. Certainly, the effects

of the poison could not be confined to the species for which it is intended. What would be the effect of the application of a poison upon predaceous and parasitic insects, birds, and predaceous mammals? Undoubtedly, these would all be affected by the reduction of their food supply that would certainly result from the application of poison, even though they suffered no direct effects from the poison. It is quite possible that the extensive

FIG. 42.—Spraying to control the elm leaf-beetle on the Capitol grounds, Washington, D. C. Note the height to which the spray is thrown. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

use of poisons in a forest might easily upset the biotic balance in such a way as to necessitate the repetition of the treatment at frequent intervals.

In the present state of knowledge, therefore, the application of poisons over extensive areas of forest cannot be generally recommended, even though it may become economically possible. It is a method that should be used with discretion. On shade and ornamental trees, however, conditions are different. Such trees are growing under artificial conditions, and, in such

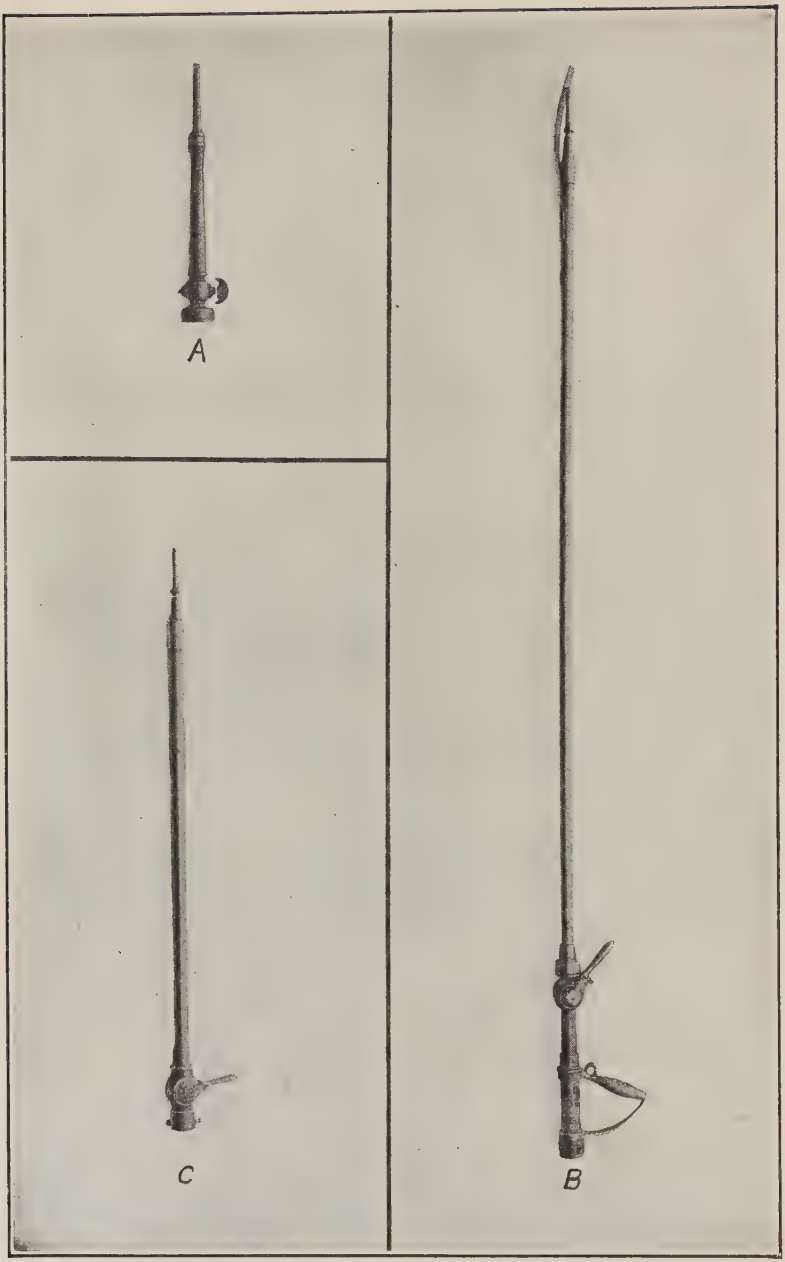


FIG. 43.—The Worthley nozzle for solid-stream spraying. *A*, old type. *B* and *C*, later types. By using one of these nozzles with a high pressure it is possible to throw a spray to the top of a tall shade tree. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

situations, the effect of environmental resistance on insect multiplication is likely to be lower than normal. Hence, it may be necessary in many instances to supplement the natural forces of biotic resistance by means of poisons. For shade and ornamental trees, therefore, the use of insecticides is an important means of protection against insect pests.

THE APPLICATION OF INSECTICIDES

Any one of several methods may be used in applying insecticides. The one selected in each instance will depend upon the kind of insect we desire to control and how it can best be reached.

Methods of Application.—Insecticides may be applied in four ways:

1. By dusting with a finely divided powder.
2. By spraying, dipping, or washing with either a finely divided powder or emulsified oil in aqueous suspension, or a chemical in aqueous solution.
3. By fumigating with a poisonous gas.
4. By means of a bait.

Each of the foregoing methods of application has its place in the scheme of insect control, and each has certain advantages and disadvantages. Dusting is wasteful of materials, but the cost of application is comparatively low. Spraying, when carefully done, and dipping are both economical of materials, but the cost of application in both cases is relatively high. Fumigation is limited in use to products that can be stored in a tight room or to small, very valuable trees that can be covered by a tent. The use of poisonous baits has received little attention in connection with forest-insect control although they have proved their value in the control of certain agricultural pests, grasshoppers for instance. It is possible that further studies of the chemotropic responses of forest pests may open the way for the development of effective baits for certain of them. A wide field of investigation is here awaiting development.

Of all the methods of applying insecticides mentioned above, spraying and dusting are in most general use at present. The other methods are little used in the control of tree insects, although some of them may have possibilities of development to the point where they may be even more satisfactory than the two methods in common use at the present time.

The Necessity for Even Distribution.—In applying insecticides, by either dusting or spraying, it is essential to success that there is an even distribution of the poisonous material. In order to accomplish this, it is requisite that the killing materials be kept thoroughly mixed with the carrier. In the process of dusting, if the poison is diluted with some inert substance, it should possess approximately the same specific gravity as does the dilutant. In liquid spraying, provision must be made for the thorough and continuous agitation of the liquid to prevent settling. Even distribution also necessitates a discharge of either the dust or the spray at a uniform rate. In a liquid spray, the finer the particles of liquid, the better will be the distribution of poison. In order to insure a fine spray and also in order that the spray may be carried to the tops of tall trees, a high pressure of from 500 to over 1,000 pounds is necessary in spraying forest trees. Because of the heavy weight of the large quantities of liquid that are required in applying insecticides in the form of a spray, this operation hitherto has been carried on from the ground.

Recently the possibility of applying poisons from the air in the form of a heavy cream-like water suspension has been the subject of experimentation, the results of which are promising. For this application an autogiro is used. This machine has an advantage over the airplane in that it can be controlled with relative ease even at low speeds (Hamilton, 1938). Both of these methods require expensive equipment. On the other hand, the application of dust to tall trees is only possible from the air, for no ground machine can blow the dust very high in the air.

CLASSIFICATION OF INSECTICIDES

Insecticides are classified not only on the basis of the methods of application but also on the basis of the methods of entrance into the body of the insect. In this latter classification there are two principal groups: stomach insecticides and contact insecticides. Frequently in entomological literature a third group is recognized: the fumigants. This type of insecticide is so closely allied to the contact type in its action that it will be treated here under that head. Two other classes of substances, which cannot accurately be classed as insecticides because their

action does not result in the insect's death, are used in insect control. These are the repellents and the attractants. The first are used to drive the insects away from the plants to be protected, whereas the others are useful in concentrating them in places where they will do no harm or where they can be controlled. They will be discussed in the following chapter.

Characteristics of Insecticides.—In most respects the two chief types of insecticides differ greatly, thus demanding separate discussion, but there is one characteristic that both types must possess and another set of characteristics the possession of which is highly desirable. The essential or requisite characteristic is a correct degree of toxicity. In order that any insecticide may be of practical use it must be sufficiently toxic to kill the insect pest but at the same time not sufficiently toxic to harm the trees upon which it is applied. One illustration of this is found in the use of arsenic. White arsenic is highly toxic to insects, but it is also highly toxic to plants; therefore such insoluble salts of arsenic as lead arsenate or calcium arsenate, which do not injure foliage, should be used in spraying, even though they are decidedly less toxic to insects than is white arsenic. The proper degree of toxicity is, then, an absolute necessity.

Both contact and stomach insecticides should, in addition, when applied as a liquid spray, possess the powers of wetting, spreading over, and adhering to the body of the insect in the case of a contact insecticide and the surface of the plant in the case of a stomach poison. The efficacy of any insecticide applied by means of spraying depends largely on the degree to which it possesses these important characteristics.

Often the distinction between wetting and spreading is not understood. The term *wetting* refers merely to the fact that a physical contact exists between the liquid and the substance wetted. But even though there is a physical contact the liquid may not spread. For instance, when oil and water are placed together there is a physical contact between the surfaces of oil and water, but a drop of water on an oil surface does not spread.

If wetting is accomplished, then the powers of a spray to spread will depend upon the forces of cohesion of the liquid, and of adhesion between the liquid and the solid. The spreading of a liquid on a solid surface is, therefore, a surface-tension phenomenon. If the force of adhesion is greater than the force

of cohesion of the liquid, then the liquid will spread over the surface of the solid. If, however, the force of cohesion of the liquid is greater than the force of adhesion between the liquid and solid, then the liquid will collect in droplets. In order to be most effective a spray should, therefore, have a comparatively low surface tension so that its force of cohesion will be less than the force of adhesion between it and the surface upon which it is sprayed. The adhesivity of insecticides applied as dust or in aqueous suspension depends upon certain physical characteristics that will be discussed later under stomach insecticides.

Stomach Insecticides.—Those insecticides that gain entrance into the body of insects by way of the mouth and the digestive tract are called *stomach insecticides*. They may be applied in the form of a dust, a spray, or the toxic ingredient in a poisonous bait. When used in the form of a dust, or spray, a stomach poison should be a comparatively stable compound that will not decompose on exposure to the air or be dissolved readily by rain. It must be capable of sticking to the surface upon which it is applied, so that it will remain on the tree long enough to permit the insects to eat a killing dose. It must also be finely divided so that it may be blown into the air in the form of a cloud or, in case of liquid sprays, so that it will be held in suspension in a liquid.

Since this type of insecticide must enter the insect's body by way of the mouth and the digestive tract, it can be used effectively only upon those insects that have biting mouth parts, inasmuch as the sucking type could not ingest a fatal dose of arsenic in the process of puncturing the plant tissues. Stomach insecticides are used primarily against defoliating insects, although in a few cases they have proved effective in poisoning young borers as these insects cut their way through the bark. Craighead (1915), for instance, has used successfully a 2 per cent solution of sodium arsenite with kerosene emulsion for this purpose. When applied to the bark of freshly cut logs or susceptible trees the young larvae were killed before they could penetrate into the phloem. Unfortunately, the arsenic, being soluble, is easily washed out of the bark by rains; therefore the treatment is often effective for only a short time.

The stomach insecticides in most common use are certain arsenicals, although some organic substances, such as nicotine, rotenone, and hellebore, may sometimes also be used. Various

experiments with silicofluorides indicate that some of this group of chemicals have high insecticidal qualities; they may prove to be both cheap and useful substitutes for arsenicals. Lead arsenate and calcium arsenate are the two compounds most universally used at present in the control of tree defoliators. Other common arsenicals are paris green, zinc arsenite, and magnesium arsenite. None of the arsenicals used as insecticides are sold in an absolutely pure condition. All of them contain small quantities of other arsenical compounds some of which are water soluble. Soluble arsenic, because it is able to penetrate and injure leaves to which it is applied, should not be used on trees. Even the small quantities contained in some of the insecticides mentioned above are sufficient to cause burning when applied to tender leaves. The two arsenicals now most commonly used, lead arsenate and calcium arsenate, contain such small quantities of this dangerous substance that their use is attended with very little danger. The others mentioned above contain larger quantities of water-soluble arsenic and hence cannot be used indiscriminately without taking proper precautions. By adding lime to the suspensions of these chemicals, the soluble arsenic combines with the lime to form calcium arsenate, which is, of course, insoluble in water. In this way some of the more uncertain arsenicals may be made reasonably safe.

Both lead arsenate and calcium arsenate are usually sold in the form of fine powders that may be applied either as a dust or in aqueous suspension. Lead arsenate may also be obtained in paste form. The powdered lead arsenate contains the equivalent of about 30 per cent arsenic oxide and usually less than 1 per cent soluble arsenic. Calcium arsenate, on the other hand, contains the equivalent of about 40 or 45 per cent arsenic oxide and is, accordingly, more toxic than lead arsenate. In using calcium arsenate there is somewhat more danger of injury to the foliage than with lead arsenate, because the calcium arsenate decomposing, as a result of a reaction with carbon dioxide in the presence of moisture, forms a soluble arsenic. Burning of the foliage may, consequently, result unless there is an excess of lime present. This kind of injury occurs most commonly when damp, foggy weather follows spraying. Calcium arsenate has, however, the advantage of being somewhat cheaper than lead arsenate.

Both lead arsenate and calcium arsenate have fairly good adhesive qualities, due in part to the small size of the particles and, in part, to their flake-like structure; even so, heavy rains are liable to wash off a large proportion of the poison. It has been shown that both the surface of the leaf and the particles of these two arsenicals carry a negative electric charge (Moore, 1925). Because opposite charges attract one another, the development of positively charged arsenicals would increase the adhesive power of these materials. Within the last few years a positively charged calcium arsenate has been perfected but has not come into general use. In order to increase mechanically the adhesivity of arsenicals, various materials are sometimes added to the spray suspension. Some of these are soap, molasses, glue, size, glucose, fish oil, linseed oil, resin stickers, and gelatin. These materials also increase the spreading power of sprays by reducing the surface tension of the liquid, thus insuring better distribution of the poison.

Contact Insecticides.—Unlike the stomach poisons that have been considered here, the contact insecticides do not need to enter the insect's body by way of the digestive tract. They enter either by way of the respiratory system, through the thinly chitinized intersegmental membranes, or through the sensory pores. In some instances, by means of their action upon the body surface, they may destroy the insect without actually entering the body. In a very few cases they may kill mechanically by plugging the tracheae and thus depriving the insect of oxygen. A contact insecticide may gain entrance into an insect's body in the form of either gas or liquid. This type of insecticide is useful against small sucking insects, like aphids and scale insects, and against leaf-mining species that cannot be easily reached by a stomach poison. It is also effective against some of the small caterpillars. It is difficult to kill the older stages of either the sucking or biting forms because of the greater resistance to poisons that the insect develops as it grows older.

The most important factors influencing the action of a contact insecticide are: (1) toxicity, (2) power to wet and spread over an insect's body, (3) low viscosity, (4) the ability to penetrate semipermeable membranes, (5) volatility.

Unless an insecticide kills mechanically by plugging the spiracles, as very few do, it is necessary, as has already been

shown, that it be toxic to insects. But the effectiveness of the insecticide is not always in direct ratio to its toxicity. Some of the other factors mentioned above are of even greater importance. For instance, if a pure aqueous solution of any material is applied to the body of an insect, it will collect in drops and run off. Such a solution, because it would not be able to reach a vital spot, would not be nearly so effective in killing the insect as a much less toxic material that would spread over the insect's body. An insecticide that tends to run off the insect's body can kill only by means of its volatile constituents, which evaporate into the air and envelop the insect in a poisonous gas even though the liquid is not in direct contact. A liquid that spreads over the insect's body surfaces, on the other hand, will penetrate into the inter-segmental areas and, also, will be drawn into the tracheae by capillarity; thus it will reach those parts where entrance into the insect's body is easiest. Contact insecticides, like stomach insecticides, may have this spreading power greatly increased by the addition of soap or some other substance that will reduce the surface tension of the spraying liquid.

The viscosity of a solution may in some instances be of importance in limiting the effectiveness of a contact insecticide. Viscosity affects not the amount of spreading but the rate of spreading. In case of a volatile material, if the viscosity is too great, the toxic principle may be lost before it reaches a vital spot. Also a viscid liquid, like a concentrated soap solution, which increases in viscosity as evaporation progresses, might solidify, as a result of evaporation, before reaching a vital part.

Another important factor determining the effectiveness of a contact insecticide is its ability to penetrate semipermeable membranes. This requires either that the material penetrate in the form of gas or that it be in crystalline solution. A non-volatile colloidal solution or a suspension, even though it contained a highly toxic material, would not be an effective contact insecticide because of its inability to penetrate through the membranes into the insect's body.

The factor of volatility is also important. The best contact insecticides not only possess the quality of wetting and spreading, but also generally contain a volatile substance; thus they have two chances of killing. They may penetrate into the insect's tissues in the form of either a liquid or a vapor. In the

latter case their action is identical with that of a fumigant. In some cases, a volatile material, like nicotine, may penetrate the tracheae in the form of a gas, condense on the walls of the small tracheae, and then penetrate through the tracheal walls in the form of a liquid. In other cases, such a material may enter the tracheae in the form of a liquid and penetrate the tracheal walls in the form of a gas. Volatility also has another important influence. A small dose of a very volatile material is not so likely to be fatal as is an equal dose of a less volatile, and equally toxic, substance. This is because of the time factor of toxicity. In the case of the very volatile substance, evaporation would take place so much more rapidly than in the case of the less volatile substance that a light dose of such a substance is likely to act merely as an anesthetic; whereas a similar dose of a less volatile, though no more toxic, substance would have remained within the insect's body long enough to have produced death.

There are many different materials used as contact insecticides; in fact, they are so numerous that it will be impossible to mention them all here. Only a few of the more important will be discussed briefly.

The most generally used of all the common contact insecticides are the nicotine preparations. Nicotine is used in the form of a fumigant, a dust, or a spray. It is also used in dips and washes. Nicotine fumigation is useful in greenhouses and conservatories. It is usually accomplished by burning paper impregnated with nicotine. Nicotine dust is made by impregnating some inactive dust, such as hydrated or air-slaked lime, with nicotine. Nicotine dust is used chiefly for a contact insecticide, but it may also have the effect of a stomach poison. It is not so effective, however, as lead arsenate. Nicotine solutions for spraying may be made by steeping tobacco leaves in warm water, but the most satisfactory sprays are the commercial extracts. These extracts contain a standard quantity of nicotine, usually 40 per cent, and can be easily diluted to the necessary strength.

Commercial solutions are sold in two forms: free nicotine solution and nicotine sulphate solution. The first is volatile and much more toxic than the second. These 40 per cent extracts are usually used at the rate of 1 part of nicotine extract to 800 or 1,000 parts of water. In spraying with these solutions, soap should be added at the rate of 1 pound to 50 gallons to

produce spreading. When soap is added to a nicotine sulphate solution, the alkali in the soap reacts with the nicotine sulphate liberating free nicotine. Thus, in this case, the soap is not only a spreader but also is an activator and increases, by a chemical reaction, the toxicity of the spray.

Many mineral oils are effective insecticides, but, because of the great variation in their chemical composition, their use in many cases has been unsatisfactory. The use of kerosene emulsion has been almost discontinued for this reason. In comparatively recent years, however, various miscible oils have come into general use. These are for the most part standard commercial products giving uniform results. They are proprietary preparations containing mineral oils in combination with a vegetable oil and an alkali to make them miscible in water. They are essentially emulsions. These materials are particularly effective against scale insects and insect eggs. The fact should be emphasized that many of them are safe only when used upon trees in the dormant condition. Highly refined white oils from which practically all the unsaturated hydrocarbons have been removed are used in the manufacture of miscible oils that are being increasingly favored for summer sprays. The saturated oils that are the base for these materials are similar to, but somewhat lighter than, the medicinal mineral oils. Although the use of miscible oil sprays is definitely on the increase such sprays should always be used with caution and according to directions.

Soaps containing a high percentage of free alkali have been used for contact insecticides. They kill by their caustic action and occasionally by plugging the spiracles of small insects. They are, at best, rather uncertain insecticides.

One of the most widely used materials for the control of scale insects and insect eggs on trees is lime sulphur. This material is composed of polysulphides that oxidize on exposure to the air. When a small insect is covered with this material, the rapid oxidation of the chemical robs the insect of its oxygen; this results in a sort of chemical asphyxiation. Lime sulphur is used also for a fungicide. It is effective against insects only in a solution of stronger concentration than is safe during the season of active tree growth; therefore it can be used to kill insects only when the trees are dormant. Concentrated commercial lime sulphur is available on the market and is the form

commonly used. Its specific gravity should be about 30°Bé. and, when used for the purpose of a dormant spray, should be diluted at the rate of 1 part of the concentrated solution to 9 parts of water. Dry lime sulphur and other forms of sulphur and lime are on the market. These substances vary greatly in effectiveness.

Hydrocyanic acid gas is a fumigant that is frequently used in treating infested nursery stock, household insects, and stored grain pests. It is a deadly gas that must be handled with great care. The gas is liberated by dropping either potassium or sodium cyanide into a 25 per cent solution of sulphuric acid. The cyanide salt is used in strengths varying from ¼ ounce to 1 pound per thousand cubic feet. One inhalation of this gas may easily be fatal to man; this material, therefore, should not be used by inexperienced people.

Certain plant substances and derivitives other than nicotine are now coming into more general use than formerly. Pyrethrins, which are substances contained in pyrethrum flowers, are highly toxic to many insects. They have the advantage of being relatively nontoxic to warm-blooded animals and more toxic than nicotine to certain insects. They have the disadvantage of decomposing rapidly on exposure to air and light. Ground debris and "cube" root,[1] which contain several active insecticidal substances, are becoming increasingly important for sprays and dusts. Some of the substances contained in these roots are rotenone, deguelin, tephrosin, and toxicarol. The first two of these are most important. The insecticidal content of the roots is variable, and therefore the results in using the powdered roots have not been constant. At present, however, it is possible to obtain tested and standardized derris-root powder. Standardized extracts are also obtainable. Rotenone is more toxic to insects than either nicotine or the pyrethrins but decomposes rapidly in air and light. These plant derivatives give some promise as stomach poisons as well as contact insecticides, but because of their cost they are not likely to replace the arsenicals for tree spraying.

From the preceding discussion of direct methods of forest-insect control, some conception may be gained of the many

[1] The name "cube" is applied in tropical America to several genera of plants used for fish poisons. Some belong to the family Sapindaceae.

means that are at our disposal for checking insect outbreaks. The method, or methods, used in any particular instance depend upon the habits of the pest on the one hand and economic conditions on the other. As has previously been pointed out, these direct methods of control are all curative in character and are chiefly applicable under conditions where the value of the trees, or of the wood products, is high. The next section will deal with indirect, or preventive, control methods.

CHAPTER VIII

INDIRECT CONTROL OF TREE INSECTS

The control of forest insects by the direct methods previously described is in its very nature expensive. Such methods call for a considerable outlay of capital, time, equipment, and materials. These operations are, as a general rule, curative in character, and are applied after the pest has become sufficiently abundant to be injurious. The indirect type of control that will now be discussed is preventive rather than curative. Under indirect control may be classed all those operations that are designed to modify environmental factors so that conditions become unfavorable for the rapid multiplication of the insects. These operations are applied, as a rule, before the insect becomes epidemic. Through a knowledge of the habits and physical requirements of insect pests, injury by them may be prevented, or reduced to the minimum. Indirect control may not be such a conspicuous victory for the entomologist from the sensational viewpoint, but it may be quite as effective and even more economical than direct control in preventing insect damage.

The application of indirect control calls for a detailed knowledge of the habits of the pests, of their relation to other organisms with which they are associated, and of their reactions to the physical elements of their environment. A much more profound and detailed knowledge of insect pests is necessary for success in indirect control, than for the successful application of direct methods. Needless to say, present knowledge is not sufficiently complete to make possible the general application of these indirect methods to all pests, but much progress in this direction has already been made; and at the present time forest entomologists, realizing the possibilities of this line of development, are devoting much effort to the acquisition of the necessary information.

For many years the use of indirect control measures has had a place in the protection of freshly cut wood. Recently, indirect

methods have also been applied to the control of insects that attack the living tree. In the following pages, there will be discussed some of the important indirect methods that have actually been applied to the control of insects of forests and forest products, and some that show promise of development. Indirect control measures may be divided into four groups as follows: (1) chemical and mechanical methods, (2) biotic methods (3) silvicultural practices, (4) statutory regulations. The first of these will be discussed at length in this chapter, while biotic methods along with silvicultural practices, and statutory regulations will be taken up in Chap. IX.

Chemical and mechanical methods of insect control are usually thought of as methods to be used only in a direct way against the insects themselves, but they may be used quite effectively in an indirect way. In most cases when used indirectly, chemical and mechanical methods operate best against pests of forest products, but in some cases green trees may also be protected. The object of these methods in all cases, when used indirectly, is to make the environment of an insect less favorable than it would otherwise be; thus, indirectly, through increasing environmental resistance, they would cause an ultimate reduction in the numbers of an injurious species. The environmental factors most commonly modified by these means are the nutritional factors of kind and quantity of food, and the physical factors of moisture and temperature. Modification by chemical or mechanical methods of each of these factors in turn will now be discussed.

CONTROL BY MODIFICATION OF FOOD SUPPLY

For control purposes, the food supply of an insect may be modified in three different ways: it may be made inaccessible by erecting either chemical or mechanical barriers; it may be made less available by reducing its actual quantity; or it may be made unavailable by changing its composition. The indirect control of insects by the modification of food supply will be discussed under these three headings.

Inaccessibility through Barriers.—Although the use of chemical barriers in the control of wood and tree insects has not been developed to a high degree of efficiency, it has been demonstrated that many of the common spray materials may be used in this

way. A number of them have a decided repellent effect upon insects; examples of these are Bordeaux mixture, lime sulphur, iron sulphate, and even whitewash. All these repel insects for a time after they have been applied. In addition to these materials, there are a number of tree paints on the market that are intended to give protection from insect attack. Most of these, however, are valueless, and some are actually injurious. In general, the use of these paints should be avoided. One very good repellent wash has been developed by Pettit (1923). This is a soft-soap mixture containing naphthalene that is effective against a number of borers, Chrysobothris, for example. Its use is limited, however, because of its drawbacks: it is difficult to mix and apply; it is rather expensive; and it must be applied several times during a season to insure satisfactory results. Still other chemicals, for example, creosote and carbolineum, applied in the form of emulsions have a strong repellent effect upon many wood borers. In some instances they have been used successfully on green trees (Graham, 1916).

The use of chemical repellents on freshly cut wood has not been practiced commercially, but experiments by Craighead (1922) have demonstrated that logs can be protected in this way. He found that spraying or dipping logs in creosote diluted with kerosene would prevent all insect attack. Ordinarily this material is too expensive for use on logs intended for lumber, but it may be profitably used in protecting rustic work, and possibly in the protection of exceedingly valuable logs intended for special uses. He also found a mixture of pyridine and kerosene, in the proportions of 1 to 10, to be highly effective for a repellent when applied to green logs. Snyder (1924) has demonstrated that creosote is an effective repellent against termites.

In the protection of trees from insect attack, mechanical barriers are sometimes used. In Europe they have even found a place in timber forests, but in America their use is confined to shade and other ornamental trees, inasmuch as economic conditions will not permit the application of these comparatively expensive means of insect control on trees intended for lumber.

The use of sticky bands to prevent defoliating insects from reaching the foliage by climbing trees has proved so effective that it is widely used in the control of cankerworms, tussock

moths, and the gypsy moth on shade trees. Such bands can be effective only against insects that reach the foliage by crawling up the tree trunks. The commercial preparation called "tree

FIG. 44.—Gypsy-moth larvae congregated on a tree trunk below a sticky band over which they are unable to crawl. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

tanglefoot" is the most convenient material for this purpose, as it can be purchased ready for use in any quantity desired. The Gypsy Moth Laboratory of the U. S. Department of Agriculture has developed a very effective banding material that is being used almost entirely in the gypsy-moth work whenever banding is done (Collins, 1920). To be effective the bands

should be watched closely to insure renewal whenever they lose their sticky quality (Fig. 44). The screening of the trunks of especially valuable shade trees has been recommended by Burke (1921) to prevent their reinfestation by the carpenter moth. That is, of course, a method too expensive to use except under unusual circumstances.

In the protection of forest products, particularly seasoned materials, the use of mechanical barriers is important. For instance, one of the most effective barriers against insect infestation is a coat of paint or varnish applied over the surface of susceptible wood. This is particularly effective against dry-wood insects, for example, the lyctus powder-post beetles (Synder, 1926). Because these beetles deposit their eggs in the open pores of seasoned hardwood lumber, a coat of paint or varnish, that closes these pores, prevents infestation.

Reduction in the Quantity of Food.—Reduction in the quantity of food available for insect pests offers an effective means of insect control, especially in the protection of forest products. This may be accomplished in several different ways. Three of the most usual are by prompt utilization, by barking freshly cut logs, and by the disposal of waste materials.

The prompt utilization of logs and other forest products is one of the most obvious methods of preventing insect injury to this class of materials, but it is surprising how often the importance of this simple means of protection is overlooked. A tree is most susceptible to insect attack just after it has been cut or killed. As the phloem region and sapwood dry out, the wood becomes less and less attractive to a large proportion of wood-inhabiting insects. The greatest amount of insect damage usually is done during the first season after the tree has been cut or has died. After that, the organisms causing decay hold the center of the stage.

For this reason, one of the most effective ways of preventing insect injury, and likewise the succeeding fungous injury, is to utilize the logs as soon as possible after they are cut; or to salvage without delay trees killed by fire, insects, or other causes before they have deteriorated. This calls for prompt action in many instances.

In the case of trees killed by a spring fire, the problem of prompt utilization is almost hopeless because the trees will be

infested with borers within a few weeks after they are burned. Unless it is possible to divert logging operations to the salvage work immediately, heavy losses cannot be avoided. When the trees are killed in the summer or fall, on the other hand, they will not be seriously injured until the following spring. In the latter instance, there is more time to plan and execute salvage operations; the mere cutting of the killed trees, however, does not mean that there will be no loss. Logging is only the first step in the process of salvage. If losses are to be avoided, the logs should either be sawed immediately or be treated by one of the methods discussed hereafter. This is particularly true of fire-killed material because of the great attraction that scorched timber appears to have for wood borers. The same rule also applies to green logs cut in the regular logging operations. The shorter the time between felling and manufacturing, the smaller will be the chance of loss as the result of insect attack. The necessity for haste in salvage is especially important with such trees as firs, pines, hemlock, and hardwoods, but is less urgent with large virgin-growth douglas fir, redwood, and sequoia (Furniss, 1937.)

By removing the bark from freshly cut wood infestation of this kind of material by wood-boring insects may be prevented, to a considerable degree. This is because many species of wood-boring insects that injure freshly cut wood, for example the pine sawyers, other Cerambycidae, and many Buprestidae, require, during the early larval period, the succulent tissues of the phloem. The young larvae of these species work in this region where the protein content is high, and where the available food materials are easily digested and assimilated. Later in their development, many of them tunnel into the solid wood, where they do their greatest damage. Because of the unfavorable conditions for borer development, the eggs of these insects are usually not deposited on healthy living trees; therefore, the wood when cut is usually uninfested. The removal of bark from freshly cut logs, pulpwood, or other wood products destroys the source of food for the early stages of these pests, and thus makes impossible their infestation of the logs.

Barking has one objectionable feature that is sometimes difficult to overcome. As the barked log or stick of pulpwood dries, the outer portions shrink more rapidly than the inner parts, with

the result that checks develop. Sometimes these checks may reach almost to the center of the logs.

Ordinarily, checking in pulpwood is of little consequence, although occasionally soot, smoke, or dust of a character not easily washed from the pulp, may settle in the open checks and cause trouble. Therefore, peeled pulpwood should be stored so that this will not happen.

Badly checked logs will be seriously reduced in value unless the checking is controlled. This is possible, at least with straight-grained logs of moderate size.

Checks always develop radially and follow lines of weakness. By hacking with an ax as deeply as possible into the peeled log along a longitudinal line, the wood will be weakened along this line, and, instead of numerous smaller checks, a single large check will develop at that point. If the log is then sawed intelligently, the loss due to checking will be very slight.

This method has been used successfully in several practical operations in the Lake states with logs up to 24 inches in diameter. Whether it can be used successfully on larger logs remains to be tested. Possibly with large logs it may be necessary to provide two or even more lines of weakness along which checks may develop.

Barking, although not as cheap as water treatment, as shown later, is not an expensive operation. The average cost in the Lake states is about 10 cents per log. This amount would be correspondingly higher, per log, in the larger timber of the Northwest, but would be lower on the basis of cost per thousand feet. Nevertheless, even though the absolute cost is not excessive, it is not justifiable under all conditions. The advisability of barking depends upon the cost of labor, the size, and the value of the logs. Without doubt it pays to bark butt logs and second cuts that are to be held over the summer, because the grade of these logs might easily be reduced from a select grade or number 1 common to number 4 common, thus causing a loss of from $50 to $100 per thousand feet b.m. On the other hand, it is doubtful whether or not barking small, knotty logs or top logs will ever be profitable, because such logs contain only low-grade materials, so that any reduction of grade by insect attack would be comparatively slight. The profitableness of barking, therefore depends primarily upon the value of the protected material.

By properly disposing of waste materials in which injurious insects may breed, many of our insect troubles may be prevented. For instance, in manufacturing plants that use hardwoods, the danger of powder-post-beetle infestation will be greatly reduced if all waste wood is promptly disposed of. The accumulation of such waste is very likely to lead to insect troubles sooner or later.

Likewise, in the forest, the proper handling of logging waste or slash is sometimes important from the standpoint of insect

FIG. 45.—Large pieces of slash left after a slash-burning operation that was regarded as being very thorough. In the usual operation much more would be left. Breeding places for most of the potentially injurious insects that live in slash have not been destroyed. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

control. The ordinary methods of slash disposal are directed primarily toward fire prevention; and as a result, only the smaller and more inflammable portions of the slash are taken care of (Fig. 45). This type of disposal has little or no influence upon dangerous forest pests, because the potentially injurious species either do not breed in logging waste at all, or else they are found only in the larger parts like the large branches, broken logs, and stumps (Graham, 1922). In order to be effective in checking the multiplication of potentially injurious insects, disposal of the larger parts by utilization, barking, burning, or some other suitable method is necessary.

The general consensus of opinion is that hardwood slash is almost never a breeding place for insects that attack living trees, and even coniferous slash is not such a serious menace as it has sometimes been regarded. There are instances, however, when coniferous slash presents important problems (Keen, 1927). As long as logging is going on, and fresh slash is continually being supplied by successive operations, the insects breeding in this material will find adequate feeding places for each generation. When logging operations end in a locality, then the slash insects, because of a scarcity of readily available food, may attack and kill standing trees or injure advance growth. Such outbreaks are usually sporadic and seldom occasion great injury.

One of the important insects that appears to be definitely associated with eastern white-pine slash is the pales weevil, (Pierson, 1921). This insect breeds in green pine stumps and injures advance growth by feeding on the bark of these small trees. The barking of stumps, in regions where this pest is abundant during the midsummer following logging, has been recommended to check its rate of multiplication, with protective results for the seedling trees on the cutover areas.

Changes in Food Composition.—The composition of an insect's food is generally very definitely limited. Each species or group of species has its own special food requirements. In view of this, whenever it is possible so to change the character of an insect's food that it is no longer suitable for its use, then another valuable means of insect control presents itself. Fortunately, this is often possible, and consequently some of the most effective control methods are based on the changing of food composition. These methods are especially applicable to the control of phloem and phloem-wood insects working in freshly cut wood. The phloem region, even at best, is suitable for the development of these insects for only a comparatively short time. If this period can be still further shortened, so that there is not time for the development of the insects, or if a change in composition can be brought about before the wood is exposed to insect attack, injury by phloem-wood insects can be materially reduced or even eliminated.

One of the ways by which wood may be protected from the attack of phloem insects is to give an opportunity for changes to take place in the inner bark before time for the insects to begin

work. This can be accomplished by cutting at the proper time of the year. Unpublished results of experiments by Craighead, and also by other workers, show decided differences in susceptibility to insect attack between logs cut at different seasons of the year. This condition is particularly true in the northern regions, where there is a long period of dormancy during the winter.

Experiments at Itasca Park, Minn., have shown that logs cut during late summer and early autumn are more immune to borer injury than are logs cut at other seasons of the year. Such logs are not immediately attacked, because no phloem insects are flying at that season. Not until the following spring, 8 or 9 months after cutting, will these insects be on the wing. By that time, changes will have taken place in the inner bark that reduce its attractiveness and desirability for use as a breeding place. Exactly what the changes are that occur during the autumn and winter is not known, although they are evidently both physical and chemical in nature. They are frequently accompanied by a change in the color of the tissues, although sometimes little apparent change occurs. When the phloem changes color it apparently no longer furnishes suitable food for the borers; but even when no apparent change has occurred, wood cut in the autumn is not so susceptible to the attack of these insects as wood of the same tree species cut in late winter or early spring.

Cutting at the most favorable time is one method of insect control that has been little developed. In view of the results of experiments, it appears possible that, in some instances, a bonus might profitably be paid by buyers for material cut in late summer, to encourage small operators to increase the material cut at that season of the year, thereby reducing the quantity of wood susceptible to insect attack.

When it is impracticable to cut wood at such a time that it will no longer contain palatable food by the time the insects fly, it may be possible to change food conditions by rapid seasoning so as to shorten the period of susceptibility. With thick-barked pieces this may be accomplished by barking. This accomplishes a double effect. It reduces the total quantity of food available for the phloem eaters, and makes possible the rapid drying of the sapwood, with the consequent food changes that soon make

the wood unsusceptible to the attack of the insects that feed in green sapwood. With thin-barked pieces, all that is necessary to accomplish rapid seasoning in many cases is to pile the wood in well-ventilated piles. This latter method is not certain in the cooler northern latitudes, however, because of a slower rate of drying. In such localities, both barking and piling in well-ventilated piles are necessary to insure rapid seasoning.

In the South, on the other hand, rapid seasoning for the purpose of modifying the character of the food, by means of sun curing of logs, has been used successfully. Under this method the pieces of wood are either piled in open piles or, in the case of logs, placed side by side on skids. In the latter case, it is necessary to rotate the logs every few days to insure even curing on all sides. The rotation of the logs not only results in hastening the seasoning rate but also results in killing directly by heat any insects that may attack the logs during treatment.

Seasoning wood for the purpose of producing unfavorable food conditions for insects is not only applicable to logs and bolts but also has its place in the protection of sawed lumber. During the process of drying, food modifications occur that prevent all future attacks of some insects, even though moisture conditions may later become favorable. Ambrosia beetles are representatives of this group. The more rapid the seasoning, the shorter will be the period during which attack by these pests will be possible. Careful piling of green lumber in such manner that there is free circulation of air through and around the piles hastens drying, but where the equipment is available, kiln drying is an even better course of procedure.

Still another means of protecting freshly cut wood from insect attack is by water treatment. The chief effect of this treatment is to change, unfavorably, the moisture conditions. This effect will be discussed in the following section. But water treatment also changes food conditions. It is a matter of general knowledge that after logs have been in water for some time they cease to provide suitable food for many wood-boring species. Logs driven in water to the mill are only slightly susceptible to insect infestation when removed from the water. Deadheads when taken out of the water are practically safe from insect attack. Craighead, in some unpublished work, has shown that a submergence of 12 months so changes the physical and chemical

nature of logs that they are no longer susceptible to infestation. Short periods of floating in water have comparatively little effect upon food composition within the wood. For this reason, short periods of driving followed by removal from the water have little or no effect either upon the insects present in the logs or upon the susceptibility of the wood to later infestation. To be effective in changing food conditions, water treatment must be continued over a period of from several months to a year.

CONTROL BY MODIFICATION OF MOISTURE CONDITIONS

It was shown in Chap. IV that one of the most important factors determining the rate of insect development is moisture. Insect development is limited by the moisture requirements of each species to a definite moisture zone. Outside this zone of moisture toleration, development is impossible; consequently, effective control of insects in logs may be accomplished either by lowering the moisture content of the logs below the limits of the insect's zone of moisture toleration or by raising the moisture content above that zone.

Reduction of Moisture.—We have seen in the preceding section that piling, barking, and sun curing are methods that may be used to change unfavorably the composition of insects' food. We shall now see that the same methods may be used for the purpose of reducing the moisture content to a point below the zone of moisture toleration. The piling of freshly cut wood in well-ventilated piles has frequently been advised in the belief that it was all that was needed to produce adequately dry conditions to inhibit the development of most insects (Fig. 46). As a matter of fact, it has been found that only logs with very thin bark will season quickly and even these, unless exposed to high temperatures in a dry atmosphere, will retain a rather high moisture content for several months. In most cases, therefore, comparatively rapid seasoning of freshly cut wood cannot be obtained except by removing the bark previous to piling. Even when this is done, the rate of drying is frequently so low that the period during which the wood is sufficiently moist to allow insect development is too long; consequently injury is sustained (Fig. 47).

If truly rapid drying can be secured, it is an effective means of control, for it operates in two directions at the same time.

Indirectly, it prevents future attack by wood-boring species and, at the same time, it directly checks the activities of insects

FIG. 46.—A pile of logs, left in the woods over the summer, heavily infested with wood-boring insects. (*L. W. Orr.*)

FIG. 47.—Pulpwood piled on dry ground awaiting shipment by boat. This wood will be heavily infested by wood borers. (*L. W. Orr.*)

that have already become established in the wood, slowing up their rate of development and sometimes even stopping it

entirely. An example of this is found in the case by which the larvae of the balsam-fir sawyer, *Monochamus marmarator*, are killed by thorough drying of the wood in which they are working. This effect has been observed by the author in attempts to rear this insect. Unless the logs are kept moist few, if any, of the beetles will emerge.

Increase in Moisture.—In many instances it is much easier to raise the water content of freshly cut wood above the point of insect toleration than to lower it below the favorable zone. We have already seen how water treatment, like seasoning, may control insects by changing the composition of their food. Now we shall see that the same treatment, with certain limitations, may be used most effectively to change the moisture content to such an unfavorable condition that insect development will be checked and sometimes stopped entirely.

There are two different ways of using water treatment. One is by sprinkling the wood with water, the other by floating it in a pond. The method selected for any particular case will depend upon existing conditions. Each has its advantages and disadvantages.

The sprinkler system has been limited in its use to pulpwood, although it could be used with equal effect upon saw logs. Under this system, during the season of insect activity, the wood throughout the pile is kept continually dripping wet by throwing water on the piles. This may be accomplished by means of an overhead system of pipes, or the water can be thrown on the piles from the ground by means of either stationary water guns or a hose. The overhead system is expensive to construct and may interfere with the handling of wood in the yard, but it is very cheap to operate because it requires a minimum of attention. The method of throwing water onto the wood from the ground requires little or no additional equipment, inasmuch as most woodyards are equipped with water mains for fire-protection purposes; but it requires a certain amount of labor in directing the stream of water. In both methods of using the sprinkler system it is, of course, necessary to provide a system of drainage to carry off the surplus water that runs from the piles of wood.

In treating wood by the sprinkler system, it should be continually borne in mind that the effectiveness of the operation

depends primarily upon the thoroughness of the wetting. Unless all the wood in the pile is kept continually wet, the treatment will have little or no beneficial effect. This system is likely to give the best results when applied to irregularly piled wood of short length. On evenly stacked piles the water is likely to run off rather than to drip through the pile.

FIG. 48.—Pulpwood stored in water at Grand Marais, Minn. This wood will not be seriously attacked by insects. (*L. W. Orr.*)

The second method of raising the water content of freshly cut wood above the point of insect toleration is, as stated above, by floating it in water. This method can be used to protect not only wood stored at the mill but also freshly cut material in the woods. There is no more economical way of preventing injury to wood that must be held over in the forest during a season or more than to get it into water.

If the wood is free from infestation when it is floated, infestation will usually not occur, especially if the logs are being worked. If it has been infested by wood borers prior to floating, the borers will develop no further and, if the wood remains in the water long enough, the insect inhabitants will ultimately be killed by the effect of excessive moisture (Fig. 48). Like most generalizations, this one sometimes has exceptions. At times, large logs floating in water may be attacked on the upper side by ambrosia beetles.

The chief objections to the floating method of protection are: (1) It is obvious that adequate water space may frequently not be available. (2) A considerable proportion of the floated wood will become waterlogged and will sink, thus necessitating either taking a loss or being faced with a heavy salvage charge.

In connection with this discussion of water treatment, other benefits than the protection of freshly cut wood against insect injury should not be ignored. Wood treated by either sprinkling or floating is protected not only against insects but also against the growth of fungi. Both stain and decay are checked or prevented by water treatment. Another benefit of water treatment is the reduced fire hazard. It is practically impossible to burn wood stored under either of the methods discussed. The danger of fire in and around the mills using one of these systems is, therefore, reduced, with the result that insurance rates are lower than under conditions where risk of fire in the woodyard is an important consideration. All these benefits of water treatment combine to make it an especially valuable means of protecting wood.

CONTROL BY MODIFICATION OF TEMPERATURE

Wood-boring insects have, as was stated in Chap. IV, a definite zone of temperature in which they are active. Within this zone the rate of development varies with the temperature. The higher the temperature, the more rapid their development. Likewise the lower the temperature, the slower their rate of development. This reaction to temperature provides us with another useful weapon in insect control. We can raise the temperature of wood above that favorable for insect development, or we can reduce it until it is below the favorable zone. In either case, the activities of the insect inhabitants will be checked.

Reduction of Temperature.—In cool climates where, even at best, there is little more than enough heat for the successful development of insects, their control in wood is sometimes possible by operations that will still further lower temperature or which will reduce the heating effects of the sun during periods when the weather is warm. The simplest way by which this effect may be obtained is to protect the wood from the effects of the sun by shading. In warm, humid climates, of course, the control of

insects by reduction of temperature is not ordinarily feasible. The smaller the surplus amount of heat, the easier it will be to check insect development by reducing temperature.

Experiments in Minnesota have shown that the temperature of logs can be much reduced by heavy shading, and that the rate of development of certain wood borers is correspondingly retarded, or even stopped entirely (Graham, 1925). The pine sawyer, which under favorable conditions completes its development in 1 year, requires from 2 to 4 years in heavily shaded logs. Chrysobothris is even more seriously affected and is unable to exist under heavy shade. Heavy shading not only reduces the developmental rate but also appears to reduce the amount of infestation of logs by wood borers. To obtain satisfactory results, however, very heavy shading is necessary. Slight shade has a tendency to make conditions even more favorable for wood-boring insects than full sunlight and frequently results in an increased rate of infestation. Thus, when shade is used to reduce the damage to logs caused by wood borers, it is essential that it be very heavy.

In the Lake states, experiments have shown that the principle of heavy shading may be used effectively in preventing the multiplication of those slash insects which are potentially pests of living trees. By piling the smaller slash over the larger parts, physical conditions in these larger parts become unfavorable for the development of the potentially injurious insects that might otherwise find favorable conditions there.

Increase in Temperature.—The control of insects by increasing temperature has a much wider possible application in direct than in indirect control, but the indirect effects are not inconsiderable. Even under conditions where the temperature does not become sufficiently high to kill the insects within the logs, intense insolation may be sufficient to prevent oviposition by most species. For this reason solar treatment may have both a direct and an indirect effect.

CHAPTER IX

OTHER INDIRECT CONTROL MEASURES

As seen in the foregoing chapter, insect numbers may be limited by chemical and mechanical methods, through modification of some of the nutritional and physical factors of the insects' environment. It is also possible, in some cases, further to increase environmental resistance by increasing the value of the biotic factors. This phase of control work will be discussed under Indirect Biotic Methods. This leaves only one of the groups of factors of environmental resistance unused by man in his attempt to prevent the too rapid increase in insect numbers, namely, the plant-physiological factors. The time is soon coming when even these little-known physiological factors are going to be the basis for protective control work by the forester. The possible use to which he may put these characteristics of trees will be discussed under the general heading of Silvicultural Practices.

INDIRECT BIOTIC METHODS

The discussion of biotic balance in Chap. V shows that in tropical climates biotic factors are of greater importance than in temperate regions in maintaining the balance. This condition probably explains the emphasis that entomologists working in the tropics and subtropics place upon the importance of biotic methods of control. In the more rigorous temperate climates there has been a tendency to depend less upon biotic methods. It was seen in Chap. VI that there are very definite limitations, at the present time, on the possible use of biotic factors in direct or curative control work, but, in the realm of indirect control, it should be possible to accomplish a great deal in the prevention of outbreaks of forest pests, by manipulation of the biotic factors of the environment. In some cases, this may necessitate the introduction of new parasites or predators; more often it will mean various activities for increasing the numbers and effective-

ness of some parasite or predator already present in the forest. In either case, of course, the object is not, as in direct control, the immediate suppression of an insect pest, but aims rather to increase the value of the biotic factors of environmental resistance so as to prevent any excessive increase in the insects' numbers. Since so little, aside from the introduction of a few beneficial species, has actually been done in this field of control, our attention will be centered, chiefly, on some of the underlying principles that should serve as a guide in the future use of indirect biotic methods.

The Use of Competition.—The first of the biotic factors, competition, has seldom if ever been consciously used by man to control insects. We should, nevertheless, not overlook the distinct possibilities of this factor as a means of insect control. In fact, it is even now in operation, although without conscious direction on man's part. Workers in the Bureau of Entomology and Plant Quarantine have, in a number of instances, noted the checking of bark-beetle outbreaks as a result of competition between bark beetles and cerambycid borers. These borers breed in the trees infested by the bark beetles and, by feeding upon the green tissues of the phloem region, rob the bark beetles of their food. When the cerambycids are abundant, the bark-beetle broods may be almost entirely destroyed. In this connection it should be pointed out that direct competition through use of food is not the only factor involved in this interrelationship, because the activities of the cerambycids beneath the bark may also hasten physical and chemical changes to the detriment of the bark beetles.

It is possible that competition, such as that just referred to, may explain in part why we seldom have outbreaks of injurious bark beetles in regions where continuous logging is being carried on. The cerambycids breed freely in logging waste and, where there is an abundance of this material, it is known that these beetles are much more numerous than in other places. Since this is true, it is logical to assume, even without recorded quantitative evidence, that competition between the borers and bark beetles is keener where slash is abundant year after year than it is under other conditions. It is possible, therefore, that, where logging is continuous, bark beetles may be affected by competition with the cerambycids.

Competition may also be observed between other kinds of insects. But here again its conscious use by man must still be left to the future. An excellent illustration of this is the effect of the European larch case-bearer upon populations of the larch sawfly. In Southern Michigan the sawfly was abundant 15 years ago, and many stands were seriously injured by this insect. The establishment of the introduced case-bearer has resulted in early spring defoliation by that insect, followed later by a shortage of suitable oviposition places and food for the sawfly at the time of its emergence. The case-bearer does not seem to damage the trees so seriously as does the sawfly, and, as a result of competition between them, the condition of the forest has been improved.

It is easy to see that when means of handling this kind of competition are found, we shall have at our command a biotic method of preventing abnormal insect abundance. Even now, though we are yet unable to direct or control this force, we can take care, in cases where this type of competition is occurring, to avoid activities that will interfere with its beneficial influence.

Control by Parasites.—The second biotic factor of the environment to be discussed here is parasites. The use of parasites in indirect control work offers great possibilities. In order to obtain wholly satisfactory results in the use of parasites in indirect control work, it would be necessary to possess a detailed knowledge of the habits and ecological relationships of these organisms. Although our knowledge is still far from complete, it is nevertheless sufficient to permit the laying down of some principles determining the effectiveness of these factors in control, and to warn us of some of the dangers attendant upon their use.

The effectiveness of a parasite in controlling an insect pest depends upon a number of characteristics. The relative importance of each depends upon the circumstances of each individual case, and therefore no attempt is made here to arrange them in order of importance. Some of the more important of these characteristics may be listed as follows.

1. A parasite should have a high biotic potential.
2. It should be synchronized with its host or hosts.
3. Alternation of hosts should not be necessary.
4. Ability to attack more than one host is to be desired.

5. It should be able to find and parasitize a large proportion of its host especially at low host density.

6. It should be able to compete successfully with other parasites when double parasitism occurs.

Seldom if ever could all of these qualities be found in any one parasite, and for obvious reasons it would be inadvisable to postpone all parasite introduction until all the ecological characteristics of each possible species has been determined in detail. Nevertheless it would seem advisable to determine the habits and general requirements of a parasite in the light of its desirable and undesirable characteristics before liberating it in an environment from which it can never thereafter be removed. Fortunately, in most instances such basic information concerning species to be introduced is now obtained prior to liberation. There is, however, considerable difference of opinion as to the relative importance of the desirable and undesirable characteristics, and interpretation of the facts does not always lead all workers to the same conclusions.

The first of the desirable characteristics listed above is the possession of a relatively high biotic potential. Obviously a high *BP* alone does not make an effective parasite, but its possession does give to a parasite the ability to multiply at a rapid rate at times when *ER* is reduced. This characteristic is important at the time of an insect outbreak and makes possible the rapid increase of a parasite under the conditions of reduced *ER* resulting from high host density. Only a parasite with a high *BP* can quickly check an insect outbreak.

Some authorities feel that the importance of a high *BP* has been exaggerated and quite correctly point out that a high *BP* is prima-facie evidence that nature has neglected the species in some other way. This is obviously true under conditions of equilibrium, when oscillations of moderate amplitude prevail, since the force of *ER* must under such conditions be equal to *BP*. When, however, the equilibrium is temporarily broken, as is the case with many forest-insect outbreaks, a parasite must be able to multiply more rapidly than its host, when the parasite *ER* is relieved by an increase in host abundance; otherwise it would be unable to overtake its host and control the outbreak before the forest suffered serious injury.

That all parasites do not seem to have the capacity to multiply at such a rate is shown by the history of such outbreaks as those

of the larch sawfly, the forest tent-caterpillar, and the spruce budworm. Although each of these insects is attacked by a number of parasites, outbreaks are usually brought to an end by a food shortage resulting from the consumption of available food rather than by the action of parasites. Not until the host rate of increase is checked by food shortage do the parasites usually overtake the host.

For instance, Tothill (1923) says of a spruce budworm outbreak in New Brunswick, Canada that started in 1912, "The rise in numbers . . . occurred when fir of suitable size for egg-laying purposes was abundant, and the diminution when the amount of the favored food plant was reduced." After 1914 the budworm population declined somewhat but still continued at a high density until 1919, when it practically disappeared. The maximum parasite population, near Fredrickton, N. B., was attained in 1918, after 4 years of excessively high host density, when 44 per cent of the host died of starvation, 11 per cent were killed by storms, 25 per cent were killed by parasites, 13 per cent by birds, and the balance by arthropodous predators.

In contrast to this Tothill also cites a case in British Columbia where an outbreak of the spruce budworm was brought under control by biotic factors without serious injury resulting to the forest. In that instance 61 per cent of the budworms were destroyed by parasites, and 39 per cent by birds and other predators. A species of Phytodietus, not present in New Brunswick, was responsible for killing 24 per cent of the host. Thus in one instance the parasites were incapable of multiplying at a sufficient rate to bring the host under control until a condition of host starvation was reached, whereas in the other instance the rate of increase was sufficient to bring about control.

It must be pointed out that the absolute rate of increase of the parasites was not a function of *BP* alone but was equal to *BP–ER*. It seems apparent, however, that *ER* must have been low in both cases cited above and that the rate of multiplication of the parasites probably attained as great a velocity as can be expected of these species under natural conditions. It seems clear that a high *BP* under such conditions as described in these illustrations would increase the capacity of a parasite to take advantage of reduced *ER* resulting from an increase in host density.

On the other hand, when balanced conditions without excessive oscillations prevail, a high biotic potential is not so essential, assuming that it is sufficiently high to exceed environmental resistance even slightly.

Another important characteristic that determines the effectiveness of a parasite is the accurate synchronization of its life history with that of its host. As a rule a parasite can attack only one stage of the host; in order to be effective, therefore, it must be ready to oviposit at a time when that stage of the host insect is available. A specific or obligate parasite, one that is limited to a single host, should have either the same length of life cycle as its host or a series of brief generations during the period of host availability. It might, otherwise, be ready to oviposit at a time when the host was not at a suitable stage. In order that a perfect synchronization between parasite and host may be maintained, it is necessary that the rate of development of the parasite either be stimulated or be retarded by the same factors that stimulate or retard the host's developmental velocity. The effect of these factors must be practically identical upon both host and parasite, or else they must both have a well-established seasonal periodicity that is synchronized.

Polyphagous habits constitute another characteristic that may determine the degree of a parasite's effectiveness. For instance, a polyphagous parasite that is synchronized with a certain pest may be more effective in controlling that pest than would be a specific parasite equally well synchronized. This is particularly true during the period following the decline of an outbreak, because at such a time the general parasite, owing to its ability to attack a variety of host species, would not suffer so greatly from a food shortage as would the specific parasite. Under such conditions, the specific parasite would be reduced in the same proportion as its host, whereas, the general parasite would be much less reduced because it could transfer its activities to other hosts. The polyphagous parasite would then be in a better position to retard the subsequent multiplication of the host than would the specific parasite. The work of Tothill (1922) concerning the natural control of the fall webworm illustrates this point. In two instances obligate parasites of the webworm were apparently completely exterminated locally following the sudden decline of an outbreak, whereas other species, although much

reduced, recovered slowly when the host again increased in numbers. It is apparent, however, that this advantage of polyphagy would apply only in cases where periodic outbreaks characterized the host, and in many instances specific parasites are very efficient.

Many parasites have several generations during a single season. In such cases, if their most abundant host is not available at all times, alternate hosts will be required. This necessity may reduce the value of the parasite because its ability to multiply is of necessity limited by the number of its least abundant host.

Perhaps the most important single characteristic that determines the effectiveness of a parasite is its ability to find and parasitize its prey, especially at low host-density. Relatively little difficulty in this respect is presented by the insects that are found on the exposed surface of trees. Such insects are usually unprotected from the attack of any parasite that may be present. There are differences, however, in the ability of parasites to move swiftly from place to place and differences in their ability to find scattered hosts. These differences have a marked effect upon the capacity of various parasite species to bring about equilibrium at a low host density. Insects that bore into the tissues of trees present a much more difficult problem. Many of the parasitic Hymenoptera are well fitted to parasitize these hidden larvae. Some of them are provided with long ovipositors, which they are able to insert through solid wood and there deposit their eggs in or on the larvae working therein. The larger species can reach a larva 1 inch or even more beneath the surface. The smaller parasites of this group cannot penetrate so deeply because their ovipositors are not so long. For this reason, they must confine their attention to borers that are near the surface. These differences have a marked effect on parasite efficiency.

In studies of the Nantucket Pine-moth, it was found (Graham and Baumhofer, 1927) that the percentage of parasitism is higher among the larvae of that insect mining in the tips of jack pine than among those mining in ponderosa pine, in spite of a lower incidence of infestation in jack pine. Perhaps this difference is due to the comparative size of jack-pine and ponderosa pine tips. The jack-pine tips are much more slender than are those of ponderosa pine. It seems quite natural that a larger proportion of the pine-moth larvae working in these slender tips would be reached by the small parasites than would be possible in the

thicker tips of ponderosa pine. The introduction of a parasite, *Campoplex frustranae*, with a longer ovipositor than those originally present resulted in an astonishing increase in parasitic control (Fig. 49.)

FIG. 49.—*Campoplex frustranae*, a very effective parasite of Nantucket pine-moth. The relatively long ovipositor makes it possible for this insect to reach and parasitize a large proportion of host larvae. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

Another characteristic that frequently influences a parasite's efficiency is its ability to compete successfully with other parasites. When two parasites of different species are brought together in the same host the stronger will survive and the other will in most instances be destroyed. The survivor may or may not be the more effective in controlling the host species. Therefore, when we introduce parasites into a new region for the purpose of controlling a pest it would seem advisable to know as much as possible about the ecological requirements of species that may be competitors, otherwise undesirable introductions may result.

At present there is considerable controversy concerning the importance of this competition between parasites. Some authorities maintain that in practice the effects of competition are usually offset by other characteristics, so that in spite of competition between species the most efficient parasite will ultimately win out, because of its ability to maintain itself at a low host density. The attainment of this equilibrium will not, according to them, be prevented but may be delayed by undesirable competition. Others feel that undesirable competition may prevent the attainment of as low an equilibrium as would otherwise be attained and in some cases may actually result in the ultimate destruction of a potentially effective parasite by one which is less efficient in controlling the host but which is a better competitor. The first group favors the introduction of all possible primary parasites, the latter favors the selection of only the most promising species for introduction.

The practical difficulty of determining the probable success or failure of a parasite in a new environment prior to its introduction has led to the conclusion by many that the only feasible procedure is to introduce first and evaluate the results later. Others warn that that such a procedure is dangerous.

In view of this disagreement among authorities it seems appropriate to limit the discussion of competition here to a description of how parasites may compete with one another.

The number of individual parasites that may reach full development in a single host depends primarily upon the size of the parasite in relation to the size of the host. In some instances many small parasites may develop successfully in the body of a large host, whereas in the majority of instances only a single parasite can complete its development in a single host. Sometimes there is a difference in the nutritional requirements of the males and females of the same species. Thus in one host the amount of food may be sufficient for the male but not for the female with the result that a differential mortality of the sexes may result in the emergence of only males of some parasites from certain species of small size. Competition may occur between individuals of the same species or between species. In this discussion we are especially concerned with interspecific competition.

The work of Pemberton and Willard in Hawaii indicates one way in which parasites may compete. In 1913 two opiine larval

parasites were introduced and both became established. One, *Opius humilis*, appeared to be most important during the years following introduction, whereas in later years the other species, *Opius* (*Diachasma*) *tryoni*, has become abundant, and *Opius humilis* has been gradually reduced in numbers (Willard and Bissell, 1926), until now on such fruits as coffee berries, in which competition is most keen, it has become relatively insignificant (Willard, 1933) (Fig. 50).

By experiment and observation it was demonstrated that double parasitism of the two species occurred frequently, and when it did that *Opius tryoni* almost always survived, because of its greater activity and aggressive use of its sharp mandibles in the larval stage (Pemberton and Willard, 1918). Whether or not this competition explains the gradual reduction of *Opius humilis* has long been the subject of controversy. It is doubtful if the available evidence is adequate to answer this question finally in either one way or the other. For the present purpose, however, it serves to illustrate the aggressive type of competition that sometimes occurs between parasites.

FIG. 50.—*Opius tryoni* ovipositing into a fruit-fly larva working in a fruit. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

Another kind of competition between parasites is described by Tothill (1922) that is no less effective than that just described but is more passive in character. In this case competition for food results in the elimination of all but one parasite. This is made possible by the habits of the parasites concerned, which live in the body of the host for some time without injuring the host greatly until just before they are ready to complete their growth and pupate. When this final stage is reached the oldest larva engages in a period of destructive feeding which results not only in the consumption of the host tissues and the death of the host, but also in the death of any other younger parasites that may be present. Thus in this sort of competition the successful parasite will be the oldest one in any individual host.

In the same paper Tothill points out that double or superparasitism occurs less frequently in nature than would be

expected. This he explains in part by the probable ability of the adult parasites to recognize and avoid the sluggish larvae that have previously been parasitized, and in part by the arrangement of the different species in more or less of a sequence so that one parasite will attack the young larvae and some the older larvae, thus avoiding to at least some degree the chances of superparasitism.

The interrelation of parasites with one another and with their host is decidedly complex, and generalizations in this connection are dangerous. It has been pointed out that the importance of the previously mentioned various desirable characteristics of a parasite varies, depending upon existing circumstances. Furthermore, a parasite may seem to have all the desirable characteristics and still be relatively ineffective because of some host characteristic. Sometimes misconceptions arise as a result of the means used to describe host-parasite relations. It seems desirable to illustrate some of these possibilities, and, for the sake of clearness, hypothetical cases will be used.

One frequent miconception concerning parasites arises from the custom of expressing the degree of parasitism in terms of percentage of the stage attacked. This is objectionable, because it tells only a part of the story. The percentage of larvae killed, for instance, means very little unless we know the relation of the larval population to the total potential population. The statement is made that 90 per cent of the larvae are parasitized. If this were the only loss in a population of 1,000,000, then parasites would have killed 900,000 hosts. But, if in previous stages of the host, 500,000 individuals had been destroyed by other causes, then the parasites would have been responsible for the destruction of only 400,000, or less than 50 per cent of the total population.

Furthermore, it is unfair to compare the effectiveness of parasites in terms of percentage of the host population destroyed, except when the population density of the host is the same for each parasite. This is because, as we have already seen, parasites are density-dependent, and vary in their ability to attack their host in direct proportion to the numbers of the host. Therefore, in expressing parasitism in terms of percentage, the relation to the total population, and the population density of the host, should be indicated.

Furthermore, the total percentage of parasitism is not significant unless we also know the reproductive rate of the host under existing physical and nutritional conditions. For instance, if the host's reproductive rate (*BP* − physical *ER*) is 10, if its maximum population is limited by available food to 1,000,000, and if the total percentage of parasitism is 90, then the number of hosts destroyed would be 900,000, leaving 100,000 survivors. But in spite of this high degree of parasitism, the reproductive rate of 10 would permit the host to maintain its numbers at the maximum number permitted by the food available. Any lower rate of multiplication by the host, or higher degree destroyed by parasites would, of course, result in a reduction of host numbers to a point where the degree of parasitism and the host reproductive rate reached a different equilibrium. An apparent instance of a continued high population in spite of a high degree of parasitism has been observed by Orr (unpublished) in connection with an outbreak of the forest tent-caterpillar, in which the parasites presumably helped to prolong an outbreak by holding down for several years the caterpillar population just within the limits of its annual food supply, thus preventing its rapid multiplication and the control of the outbreak by starvation.

From the previous discussion it might be inferred that food limitations as represented by the relative abundance of the host are the only factors of *ER* that are operative to restrict parasite populations. This is of course not true because these, like all other insects, are affected by the physical elements of the environment. Likewise parasitic insects are subject to the attacks of predators and other parasites. The parasites that attack other parasites are known as *hyperparasites* in contrast to the *primary parasites* that attack nonparasitic hosts. Hyperparasitism has been known to occur to the fifth degree. As a rule this sort of multiple parasitism does not occur with sufficient frequency so that it is of much economic importance although occasionally it may be.

At the present time, the principal use of parasites in the indirect control of insects in America is the introduction of exotic species. This work is being conducted, for the most part, by representatives of the Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture, the State of California, and the

Entomological Branch, Canada Department of Agriculture. In most instances, the insects against which the work is directed are agricultural or horticultural pests that have been introduced accidentally into this country from other parts of the world. Some of these are the alfalfa weevil, the European corn-borer, the Mexican bean-beetle, the Japanese beetle, and the brown-tail moth. One forest pest, the introduced gypsy moth, has received a great deal of attention. Large sums have been spent annually in the collection in foreign lands, in investigation, and in colonization of parasites of the gypsy moth and its associated horticultural pest, the brown-tail moth for a period of over 30 years, with the result that some 60 species of foreign parasites of these insects have been introduced. Of these, about 16 species have become established in this country and are now helping to control the insects. Seven or eight of these have become abundant and promise to be important. Just how effective they will ultimately prove to be remains to be seen, but it is not likely that they will become any more effective than they are in Europe, where occasional outbreaks of the gypsy moth occur in spite of the presence of its parasites. But even though the parasites do not come up to the expectations of some enthusiasts, they will certainly bring about an increased environmental resistance that will be helpful in reducing the frequency and severity of gypsy-moth outbreaks.

In the work of introducing parasites, an attempt has been made to bring in every primary parasite that has any promise of being effective (Burgess, 1926), on the theory that the more of these enemies present the greater the probability that one or more of them will be ready at any time to check an increase of the moth. The chief basis for this theory is the fact that no one species of parasite controls the moth in any part of its native range. Furthermore, in different localities different parasites are important. This theory is quite logical in so far as it applies to parasites that are supplementary in their action, but, when the multiplication of species leads to the introduction of competing species, the results may be open to question.

In view of the dangers attendant upon the introduction of parasites, the greatest caution should be used in this work. Care should be exercised to avoid the introduction of parasitic species that may be hyperparasites. This calls for a detailed knowledge of the habits of these insects. The introduction of

species that will compete directly with species already present should as far as possible be avoided, unless it is certain that the new species will be more effective than any of those already established. Care should be used, when a choice of species is possible, to select for introduction those parasites that promise to be the most effective and the best suited to the environment in which they are to be placed. The selection can be made with safety only after careful ecological studies have been made of the parasites, the hosts, and the environment.

The introduction of parasites has been used primarily in connection with the control of introduced pests, but it is possible that species may be found that will be an aid in checking the rate of multiplication of some of the native pests as well. The way in which the tachinid parasite, *Compsilura concinnata*, introduced as a parasite of the gypsy moth, is now attacking more than 115 native species is an indication of some of the possibilities that should not be overlooked (Howard, 1922).

When introduced parasites once become thoroughly acclimated and established, they take their place in the new environment where, like any native species, they serve as a natural check for pests. The effectiveness of both native and introduced species can be increased, to a certain extent, by certain methods of silvicultural practice. These will be discussed later in this chapter.

Control by Predators.—The part that predators play in environmental resistance has been previously discussed. Although no one doubts the value of this group in maintaining a check on insect numbers, the use of predators in supervised control work has received entirely too little attention. In fact, in actual forest practice in America, comparatively little consideration is given at present to these important control agencies. This condition must be changed if we are to take advantage of all the possible means of preventing the ravages of forest insects.

Predators have been used indirectly in several instances with successful results. Examples of this are the introduction into New England of the fiery hunter, *Calosoma sycophanta*, which aided in the control of the gypsy moth, *Porthetria dispar*, and the introduction and establishment of certain Coccinellidae, the vadalia beetle, for instance, in the California citrus region, with great success in the control of scale insects. Because these predators are better suited for the work of control than any of

our native species, they are a valuable addition to our fauna. The fiery hunter, for instance, although it is a carabid or ground beetle, is unlike any of our native species in habit. The larvae of this insect, instead of staying on the ground like its relatives,

FIG. 51.—A burlap band placed around a tree to attract the congregating gypsy moth larvae to a point where they can be killed. Larvae of the fiery hunter are feeding upon the gypsy moth caterpillars. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

are able to climb trees in search of their prey (Fig. 51). Because of this ability, the fiery hunter is able to feed upon arboreal caterpillars, and is very useful not only in helping to hold down the numbers of the imported gypsy moth, but also helps to check the multiplication of native caterpillars.

The introduction of vertebrate predators is attended with somewhat more evident risk than is the introduction of invertebrates, because of the greater flexibility of habit and the greater

powers of mobility characteristic of these predators. We have a number of examples that should make us cautious in introducing such predators without carefully studying the situation beforehand. The English sparrow, for instance, was introduced to control certain hairy caterpillars, and has become a pest in certain parts of the country. The mongoose in some of the West Indian Islands (Williams, 1918) has destroyed the snakes that it was introduced to destroy, but is now making poultry raising in these islands impossible. Nevertheless if predators are selected only after careful consideration, the dangers attendant upon their introduction may be minimized.

Before man can make full use of predators as an instrument to check insect pests, much data must be collected regarding the relations existing between predators and the rest of the environment. In the meantime, the least he can do is to see that, in so far as is possible, no silvicultural methods are put in practice which will tend to reduce the numbers of beneficial predators already present in any environment. Anything he can do along silvicultural lines to make conditions favorable for their natural increase will be just that much gained. The possibilities existing along these lines will appear in the following section.

SILVICULTURAL PRACTICES

It has already been seen that the control of insects by mechanical or chemical methods has limited possibilities of application. This is in part due to the expensive character of these operations and in part to the inaccessibility of many forest areas. With the application of more intensive methods, the latter of these difficulties will be largely removed, but it is doubtful if even then chemical or physical methods of insect control can be applied to extensive forest areas. It has also been seen that the biotic factors of the environment offer decidedly favorable possibilities as indirect means of combating insect pests of the forest, but that these have not been developed sufficiently to accomplish the results for which they have been striving. Whenever possible the breaking of the biotic balance must be prevented, so that control measures for its restoration will not be required. This work of aiding in the preservation of a balanced condition can best be brought about by silvicultural practices.

It has long been recognized by foresters that a forest growing under natural conditions is less subject to insect attack than is one where natural conditions have been disturbed. This means that a forest in which the various environmental factors have come into a state of equilibrium is safer than a forest in any other condition. Here is the fundamental keynote for silvicultural practices, which will make the use of ordinary control measures largely unnecessary. If trees are grown under such conditions that the biotic balance is maintained throughout the rotation, there will be no need to resort to costly measures to restore a broken balance.

This is not so simple as it may first appear to be. The factors that react to produce the conditions of balance do not always have the same values at every stage in the development of a forest. As the trees grow and crowd out first the grass and weeds, then the underbrush, and later certain trees, the food factor varies in both quality and quantity. Also as the trees develop, the physical conditions within the forest vary, and the animal life of the forest is modified accordingly. But throughout this developmental period, during which the environmental factors are continually changing in value and in their relation to one another, because the variations are compensating, the balance between biotic potential and environmental resistance will normally be maintained. If this were not true, it is evident that a forest could never reach maturity, because it would certainly meet with some calamity in the form of a pest before many years of the rotation had elapsed (Graham, 1938). The aim of the forester, therefore, should be to develop methods of silvicultural practice that will maintain the biotic balance. If he is successful in this effort his forest will not suffer from insect outbreaks.

To accomplish this end, it is necessary to have an accurate knowledge of the environmental factors involved. At present, the knowledge of these factors is decidedly limited, and it will be many years before they can be handled with precision. In spite of this ignorance it is not necessary to despair, for there is a plan that has already proved itself to be successful in the virgin forests. This plan is the one followed in the development of the virgin forest as it originally occurred in each forest region, type, and site. Later the accumulation of data will probably make possible the development of modifications of nature's plan that

will better answer the requirements, but for the present it should be attempted, as nearly as possible, to pattern the forests of the future on those that have proved themselves successful in the past.

Regulation of Forest Composition.—Too often, even in regions where mixed natural forests are the rule, foresters have made the mistake of concentrating their efforts in the establishment of a single species of tree over large areas. Such an effort is doomed, eventually, to failure, unless it is economically possible to substitute for the force of environmental resistance, lost by the change of forest composition, an equal force in the form of control measures. The sad plight of the Saxon forests, once the pride of European forestry, illustrates well the ultimate fate of the artificial pure forests. As a result of the nun-moth outbreaks accompanied by soil depletion and other unfavorable conditions, these forests of pure spruce are at present in a desperate condition.

Only those species of trees that normally grow in pure stands can be handled safely in pure stands. Many of the two- or three-leaved pines, for example, ponderosa pine and jack pine, are rarely found in anything but pure stands. In such cases, a condition of balance has been established between the trees, the ground cover, and the pests. In these natural pure forests, therefore, it is just as necessary to preserve this balance by protecting the entire floral composition, including trees, herbs, and shrubs, as it is to preserve the original composition of the mixed forest. Overgrazing either by wild or domestic animals, ground fires, the introduction of exotic game animals, in fact, any force that will result in a modification of the ground cover in natural pure stands, should, as a general principle, be guarded against. Either overgrazing or ground fires may so reduce the variety of the flora, and thereby the total number of phytophagous insects in a region, that insectivorous predators will not be able to find sufficient food at certain seasons of the year; their numbers will consequently be reduced, with the result that some one insect upon which they normally feed at another season may be able to multiply in such great numbers as to do serious damage to the forest.

It should be recognized that, in the long run, in nature all forces combine to prevent the favoring of one species at the expense of others. Whenever, by some combination of cir-

cumstances, one species does come to dominate an environment, as is the case in the climax-type pure forest, sooner or later nature brings about a reduction of such a species. This is often accomplished by an insect outbreak; thus, outbreaks may arise as a result of the action of natural forces without the interference of man. In the managed forest, it should ultimately be possible to prevent such outbreaks and, eventually, to produce a forest that will be safer from insect outbreaks than even the natural forest.

The disastrous results rising from failure to regulate forest composition may be found many times in the annals of forest entomology. Perhaps one of the best examples of this is to be found in the spruce-budworm outbreaks that devasted the spruce-balsam stands of eastern United States and Canada between 1909 and 1920. A detailed discussion of this insect will be taken up later, but a few of the salient features may well be introduced at this point. All the available evidence appears to prove that this great series of outbreaks, which destroyed over 200,000,000 cords of balsam fir and many million cords of spruce timber, arose as a result of the type of forest developed in the infested region by a combination of unregulated, or improperly regulated, cutting operations, forest fires, and natural succession. These agencies produced a forest that contained a very high percentage of balsam fir, the most suitable food tree of the spruce budworm. This change reduced the environmental resistance by improving food conditions and, probably, by decreasing the natural enemies of the budworm to a point where rapid multiplication of the pest was possible. Regulation of forest composition is the obvious way by which this insect may economically be kept from overabundance.

Another illustration of the effect of forest composition upon the susceptibility of trees to insect attack is to be found in the jack-pine situation in the Lake states. This species of tree was originally confined to the very poor, sandy lands where other species of pine could not grow. Although the tree occurred normally in pure or nearly pure stands, this type was broken up into comparatively small areas interspersed with other forest types. As the virgin stands of white and red pine were cut, the jack pine extended its domain and became the predominant tree over vast areas that had been originally occupied by other

species of pine. In the original condition, jack pine was notably free from insect injury and was regarded as being a resistant species. In the past 20 years, however, it has suffered severely from at least three defoliating insects and one serious scale insect. With the right combination of weather conditions, serious insect outbreaks cannot be avoided. Inasmuch as the weather cannot be regulated, an attempt should be made to bring about conditions that will be reasonably free from the danger of insect outbreaks regardless of the fluctuations of weather. For this reason, it is imperative that the jack-pine areas be reduced to approximately their original status by silvicultural means.

There are a number of other interesting examples of outbreaks in regions where forest composition has been changed by logging or fires. Among these are the forest tent-caterpillar, in the oak and aspen regions of the Lake states, and the walking sticks, in the oak forests of Michigan. In each case the same set of conditions preceded the outbreak: an increase of the food for the pest combined with a decrease in the number of the natural enemies of the pest. In these pure second-growth forests the food conditions for birds, and other predaceous animals, are decidedly more limited than they were in the original, mixed forest. At present, food in these forests is sometimes abundant whereas, at other times, it is very scarce. Because the abundance of an animal is limited by the amount of food available during the period of greatest scarcity, the predators, like the other forms of life in these pure forests, are comparatively scarce. This scarcity is most easily seen among the birds, but it also applies to predaceous insects. Such a reduction in the number of predatory forms must necessarily reduce the effect of environmental resistance upon phytophagous insects. Under such conditions, it should, naturally, be expected that an overabundance of insects is much more likely to occur now than formerly.

Regulation of Density.—In addition to the regulation of forest composition, there are a number of other silvicultural means by which environmental conditions may be regulated with the result that the harmful activities of forest insects will be reduced. One of these is the regulation of forest density. The importance of density has been shown in the case of a number of forest pests, especially the white-pine weevil, *Pissodes*

strobi (Graham, 1926). This insect will be discussed fully in a later section.

Forest density influences the physical conditions found in the forest by modifying such factors as light, evaporation, air movement, and temperature. This, of course, has an indirect effect on the insect life in the forest. Although the effect of these physical factors is evident from general observation, specific data concerning their effect on insect life in the forest are very scarce. Meager as the knowledge along this line may be, it is known that many of the sun-loving beetles are attracted only to those trees or parts of trees that are exposed to the direct rays of the sun; for instance, the work of the two-lined borer, *Agrilus bilineatus*, is almost entirely confined to shade trees or to trees growing in open stands or to the few exposed branches in a fully stocked stand (Chapman, 1915). The same thing is more or less true of the bronze birch-borer, *Agrilus anxius*, and many other species.

Degree of density is also important in determining the ability of forest trees to outgrow injuries to their terminal shoots. In a fully stocked stand, there is a stimulation to straight growth, whereas in a scattered stand this stimulation is much less powerful. Furthermore, proper spacing tends to maintain the trees in a healthy condition, and consequently, as a general rule, makes such trees either less susceptible to insect attack or better able to outgrow injury.

Selection of Site.—Another important consideration, from the standpoint of silvicultural protection from forest insects, is the selection of site. Under favorable conditions of site, a tree is able to withstand a much greater amount of injury than it could if growing under less favorable conditions. Craighead (1925) has shown that balsam fir is much more resistant to injury by the spruce budworm when it is growing on a favorable site than when it is growing under poor conditions. He goes so far as to recommend growing this species in pure stands, on sites where the tree grows rapidly, in spite of the budworm menace. It has been questioned whether or not such a recommendation is justified. But the fact remains that vigorous trees survived the budworm outbreak when growing in either mixed or pure stands, whereas less vigorous trees in the same region were almost all killed.

The same is true of other insects. From observations in Minnesota, it appears that thrifty, fully stocked forests are, as a rule, immune to the bronze birch-borer, *Agrilus anxius*. This insect becomes injurious only in a fully stocked forest after the rate of growth has been reduced because of overmaturity, competition, or poor site conditions. Much of the second-growth white birch in the Northeastern forests is growing on poor soils, and for this reason Agrilus is likely to prevent most of these stands from attaining full development.

In the West, site is of considerable importance in determining the susceptibility of trees to the attack of bark beetles. For instance, the western pine-beetle, *Dendroctonus brevicomis*, is much more injurious upon ponderosa pine growing on comparatively poor sites than it is upon the same species growing under more favorable conditions.

Regulation of Drainage.—Sometimes a site is poor because of an excess of surface water. This may result in an acid soil and other conditions which inhibit growth. In some cases these conditions may be improved by the construction of a superficial drainage system to carry off the excess water. Such operations, if they result in a stimulation of growth and the general improvement of the vigor of the trees, will reduce their susceptibility to insect injury.

Another effect that drainage may have in the case of swamp forests is to change conditions of ground cover. There is some evidence that such a change may have an effect upon the overwintering stage of pests that hibernate in the layer of the duff or in the surface vegetation (Graham, 1928). For instance, if certain tamarack swamps were drained, the surface vegetation of moss and grass would give way to other plants and become more varied. This change in the vegetation by improving food conditions would, in turn, bring about an increase in the number of mice per unit area. Mice destroy large quantities of larch-sawfly cocoons and their increase, as an indirect result of drainage, will aid in reducing sawfly abundance. Furthermore, it has been shown that hibernation of the sawfly is most successful in the sphagnum hummocks that are so common in tamarack swamps. It is probable, therefore, that a change from the sphagnum ground cover to one representative of dryer land, resulting from drainage, would produce conditions less favorable for hibernation

than those now prevailing. Still another effect of drainage is the stimulation of tree growth. This effect is evident in many partly drained swamps and makes the trees better able to survive partial defoliation.

Selection of Resistant Varieties and Species.—In the foregoing sections, it has been stated that any practice resulting in the production of vigorous, rapidly growing trees helps to increase the resistance of the trees to both attack and injury. It is a matter of common knowledge among foresters that all individuals of a species do not respond equally well to favorable conditions. Some of them will grow more rapidly than others even under practically identical conditions. This ability of some trees to grow better than others is apparently due to physiological qualities within the trees themselves, which, if we are to judge from other plants, are probably genetic in character and can consequently be transmitted from generation to generation. If this is true, then the selection of especially vigorous strains not only will result in a greater production of wood products, but also may increase the resistance of the trees to insect attack and injury.

Much has been accomplished in agriculture and horticulture in the selection, breeding, and propagation of trees and other plants possessing desirable characteristics, but in forestry little has been done along this line. The possibilities of developing strains that will be resistant to the attack of certain fungous diseases are beginning to be realized (Hartley, 1927), but the possibility of selection for insect resistance has been almost entirely disregarded.

That there are great possibilities along this line cannot be doubted, but, at the same time, it must be admitted that there are many difficult problems to be solved in the technique of breeding forest trees. For the present, the best that can be done is to select seed for propagation from trees that have those qualities that are desired. By the gradual elimination of undesirable individuals we can cause to a greater and greater degree the fertilization of the desirable trees by other equally desirable individuals and thus continually improve the strain.

Some of the possibilities of reducing insect damage by selection of resistance trees have been indicated in the discussion of physical factors of environmental resistance in Chap. IV. For instance, the individual norway-spruce trees that are unsuscepti-

ble to adelges attack may serve as a nucleus for the development of a resistant variety. Likewise, the individual trees that show a resistance to nun-moth attack may provide the parent stock for a nun-moth-resistant strain. The development of pines having an unusual ability to produce resin may also serve as a means of reducing the susceptibility of our pine forests to the attack of dendroctonus beetles. In instances such as those just mentioned, the desirable characters are more or less definite and can be seen or proved to exist by means of tests; consequently, the trees that exhibit these characteristics may be selected without hesitation. In other cases it is not so easy to determine just what characteristics are responsible for the resistance to insect attack or injury.

Sometimes trees may be selected for their resistance to attack, but in other instances selection may be based on the ability of certain trees to overcome injury. An example of this possibility has been shown in connection with studies of the Nantucket pine-moth (Graham and Baumhofer, 1928). This insect shows little or no discrimination in attacking trees. In ponderosa pine plantations at Halsey, Neb., the trees are all attacked with about equal severity. From this it might appear, at first glance, that selection of resistant trees for pine-moth control would offer little promise of success. But in spite of the uniformly heavy pine-moth injury certain trees were much larger than others of the same age. Some might have been 6 or 8 feet high while others of the same age, and only a short distance away, were only 1 or 2 feet high. The tall trees have demonstrated their ability to grow in spite of injury, whereas the others have failed under the test. By selecting for seed trees those individuals which have made the best growth under conditions of heavy attack and by destroying before they begin to bear pollen those that have shown themselves to be unsuccessful under such conditions, a strain of ponderosa pine comparatively resistant to pine-moth injury may perhaps be developed. Certainly, the development of resistant varieties of trees is a line of endeavor that should no longer be neglected.

There is a possibility that the selection of comparatively resistant species may, in some instances, be more simple and at the same time as effective as the development of new varieties. This possibility was also brought out in the Nantucket pine-moth

study: The different species of pine exhibit susceptibility to attack and injury in varying degrees. For instance, austrian pine is only slightly injured; scotch pine and jack pine are freely attacked but are able to overcome the injury, whereas ponderosa pine is highly susceptible to both attack and injury. If it were not for the fact that both austrian and scotch pine are, for other reasons, less desirable trees for sand-hill planting than the ponderosa pine, their substitution for that species in the Nebraska plantations might be desirable.

Another case in which selection of resistant tree species may be used as a means of protecting forests from insect attack is in the protection of certain forests from injury by the gypsy moth (Mosher, 1915). By reducing the proportion of particularly susceptible species, like oak, aspen, basswood, and a few other less important species, the danger of injury by this insect will be greatly reduced (Behre, 1936).

From this brief discussion of the relation of silvicultural practices to the abundance of forest insects, it can be concluded that herein lie great possibilities for economical and effective maintenance of balanced conditions in our forests. The possibilities along this line are limited primarily by the knowledge of the factors that regulate all the forms of life in the forest.

STATUTORY REGULATIONS

Examination of a list of the important insect pests of the United States and Canada reveals that numerous enemies of the forest have been introduced from other lands. Outstanding among these are the gypsy moth, browntail moth, poplar weevil, European spruce-sawfly, elm leaf-beetle, larch case-bearer, and possibly the larch sawfly. Statutory regulations designed to prevent or retard the spread of noxious species from one locality to another have assumed important proportions since 1912, when Congress passed the first quarantine act (Strong, 1938).

Quarantines and Embargoes.—Quarantines are designed to regulate the movement of products from one locality to another in such a manner that the introduction of pests into uninfested localities will be either prevented or retarded. Embargoes prohibit the entry of products from localities where a certain pest is known to occur (Wardle, 1929).

Although the original idea behind the federal and various state quarantine acts was to prevent indefinitely the introduction of noxious insects into uninfested localities, the possibility of accomplishing this has frequently been questioned. Although the inspection service of the United States is very efficient, the difficulties of inspection are inevitably tremendous. Infested materials may be overlooked by even the most conscientious and well-trained inspector and allowed to enter. The treatment of materials by fumigation, heat, or other methods may fail in some instances, or unsuspected pests may enter in an undistinguishable stage or in unsuspected products.

When the volume of plant products moving between different countries and between states, the complexities of international trade, and the ever-increasing speed of transportation are considered, it seems almost inevitable that ultimately all species will reach every spot on the earth where conditions are suited to them.

This does not mean that quarantines and even embargoes are necessarily undesirable, but, like other control measures, they should be evaluated in terms of values saved. If, by a quarantine, a crop is protected from a potential pest for even a few years, the expense of the quarantine may be entirely justified. Furthermore, during the period of effective quarantine against some pest, research and increasing technical developments may result in improved control procedures that will reduce the seriousness of the pest's ultimate introduction.

Wardle (1928) suggests that a plant protection service "for the detection of initial outbreaks and for the radical eradication of initial outbreaks" might be more effective than the attempts to keep out insects that ultimately will enter in spite of the quarantine. Such a protection service would certainly be tremendously expensive, but it is possible that it could prevent enough damage to justify its maintenance for species that are economically controllable by direct means.

Inspection and Certification.—The establishment of quarantines between countries and between states or provinces within countries has forced local authorities to clean up dangerous situations in order to avoid embargoes on their products. The various state inspection services attempt to prevent the shipment of infested stock from nurseries and otherwise guard against the distribution of noxious insects from place to place.

In most states, all plant products must be inspected and certified to be free of dangerous pests before they can be accepted by common carriers for shipment. In some states, it is illegal to dig up and transport, in any manner, wild plants without inspection and certification. These inspection procedures are, perhaps, the most valuable outgrowth of quarantines and contribute much to check insect spread through commerce.

Forest planting stock is usually inspected in the nursery. If the nursery is found to be free of dangerous pests, a certificate permitting shipment of the stock is issued. If infestations are found, certification is withheld until the infestation has been cleaned up. Precautions to prevent possible infestation of nurseries are recommended or, in some instances, required. For instance, a conifer-free zone around commercial nurseries producing coniferous planting stock is required in Minnesota in order to reduce the danger of infestation from adjacent trees. This is a desirable procedure for nurseries that ship their trees outside their immediate locality, but seems unnecessary if the trees are to be planted locally.

In spite of all possible precaution, insects may escape the observation of the inspector and be transported to uninfested localities on nursery stock. For this reason, it would seem desirable, especially in forest planting, to avoid shipping stock from one region to another. The Nantucket pine-moth and the jack-pine soft-scale were both shipped into Nebraska on nursery stock and have there caused great damage. The introduction of both these pests could have been avoided or postponed for many years if planting had been postponed a year or two until stock could have been grown locally from seed.

At present, the U. S. Forest Service is following the wise policy of establishing local nurseries to supply local needs. With the demands for planting stock thus provided for, it should not be necessary to ship stock outside the locality in which it is grown, thus avoiding one source of the introduction of new pests.

CHAPTER X

LEAF-EATING INSECTS

The foliage of trees furnishes food for a host of insect species. Many of these are dangerous forest pests but, fortunately, the majority of the leaf-eating insects usually occur in comparatively small numbers. When they are not numerous they will scarcely affect the welfare of the trees, because thrifty trees always have a greater amount of foliage than is actually required for their maintenance. When, on the other hand, some leaf-eating species multiplies so much more rapidly than it can be reduced by environmental resistance that it attains tremendous numbers, as sometimes happens, the resultant defoliation will seriously injure or even kill the trees attacked.

DEFOLIATION

Sometimes these outbreaks of defoliators apparently arise with amazing suddenness. For instance, the latest outbreaks of the spruce budworm appeared to burst out over wide areas the same year. This was true also of the outbreaks of the larch sawfly. Careful observations will prove, however, that such outbreaks are probably not so sudden as they appear to be. In the case of defoliators, the failure to observe the increasing injury caused by growing numbers of insects may be explained in part by the inconspicuousness of light defoliation. A tree may be stripped of from 25 to even 50 per cent of its foliage without appearing greatly abnormal, provided the defoliation is evenly distributed over the entire crown of the tree. This is illustrated in Figs. 52, 53, 54, and 55. Figure 52 represents a normal larch tree in full foliage, Fig. 53 shows the same tree after 25 per cent of the leaves had been mechanically removed, Fig. 54 shows the same tree with 50 per cent of the foliage gone, and Fig. 55 shows 75 per cent defoliation. Defoliation is not noticeable until the greater proportion of the leaves has been destroyed. When once one realizes the large numbers of an injurious species that may be

present unnoticed in a forest, and then considers the tremendously great possibilities of their extremely rapid reproduction under favorable conditions, the occurrence of apparently sudden outbreaks can be more easily understood. For instance, field studies of the spruce budworm indicated that, under favorable circum-

FIG. 52. FIG. 53.

FIG. 52.—A tamarack tree in full foliage.

FIG. 53.—The same tree as that shown in Fig. 52 with 25 per cent of the foliage mechanically removed, showing how inconspicuous evenly distributed defoliation may be.

stances, this insect may increase a hundredfold in a single generation. At this rate, defoliation might increase from an inconspicuous condition to almost complete defoliation in 1 or 2 years. Such outbreaks are the result of a disturbance in the biotic balance. They are particularly common where the character of the forest has been modified by the action of some external force such

as fire, wind, or the operations of man, or where natural succession has brought about the establishment of the so-called *climax forest type* over large areas.

Effects of Defoliation.—Defoliation injures trees by stopping or checking the elaboration of food materials by the photosyn-

FIG. 54. FIG. 55.

FIG. 54.—The same tree shown in Fig. 52 with 50 per cent of the foliage removed. Even this amount of defoliation is not especially conspicuous.

FIG. 55.—The same tree shown in Fig. 52 with 75 per cent of the foliage removed.

thetic process, by interfering with transpiration, and, probably, by interfering with the processes of translocation of food within the tree. A combination of these effects is reflected in the rate of growth. Defoliation has such a profound effect upon growth that it is possible to trace the history of past outbreaks of leaf-eating insects by studying the annual rings of the surviving trees. Studies of the effect of spruce-budworm defoliation upon the growth of balsam fir and spruce made by Craighead (1924)

have proved that growth as a whole is reduced the first year of defoliation. Growth at the top of the tree is usually very much reduced, but at the base it is usually greater than in the years immediately preceding defoliation. Investigations made by the author in budworm-infested areas, other than those studied by Craighead, go further to prove that a widening of the annual ring at the base of the tree, combined with a narrowing of the same ring at the top, is the usual occurrence during the first year of defoliation. After the first year of defoliation the rings at the base, like the corresponding rings at the top, become successively smaller and smaller, until they are often so narrow that the individual rings cannot be distinguished without the aid of a magnifier. In some cases, under conditions of very severe defoliation, there may be no production of wood for a season or more, in which case rings may be entirely absent. In other instances, wood may be laid down in certain parts of a tree and not in others. This results in the production of incomplete rings. Great care must therefore be exercised in assigning a definite year to a specific ring during periods of defoliation. If a tree survives defoliation, recovery is always gradual. As the foliage is gradually replaced, from year to year, the width of the rings increases in similar proportion, until a normal rate of growth has been attained. Similar ring pictures occur in other species than balsam fir and spruce as a result of defoliation, except that it is sometimes difficult to demonstrate the widening of the basal ring of the first year's defoliation.

All species of trees are not equally susceptible to injury from defoliation. Hardwoods are relatively resistant and will often successfully withstand 3 or more years of defoliation. This is due to their relatively large supply of stored food, which results in a comparatively rapid replacement of foliage. Correspondingly great resistance to injury from defoliation is also characteristic of deciduous conifers, as exemplified by the larch. Evergreen conifers, like balsam fir or spruce, are more easily killed by this type of injury; for instance, white spruce, hemlock, and probably many others will die as a result of a single complete defoliation. As a rule, more than 3 successive years of defoliation is fatal even to broad-leaved trees.

Resistance to defoliation injury varies not only with the species but also with different individuals of the same species. Domi-

nant trees are decidedly more resistant than suppressed individuals of the same species; likewise, trees growing with little or no competition are more resistant than trees growing under less favorable conditions. The reason for this is to be found in the fact that dominant trees and trees growing in the open with-

FIG. 56.—Typical work of the birch-leaf skeletonizer, *Bucculatrix canadensisella*, on paper birch. (*University of Minnesota.*)

out competition have larger reserves of stored food than those growing in competition with, and those suppressed by, other trees. This large reserve makes it possible for such trees to replace destroyed foliage. If defoliation continues after the exhaustion of stored food, a tree is sure to die.

The first parts of a tree to die as a result of loss of foliage are the extremities, the twigs, and small roots. Craighead (1924) has shown with balsam fir that when the roots have been severely injured the tree is almost certain to die. The same condition

appears to hold for at least some other conifers, for example, jack pine, and may apply to conifers in general.

Trees that have been reduced in vitality by defoliation are much more susceptible to the attack of bark beetles or borers. Frequently trees that might survive defoliation are killed by

FIG. 57.—The spiny elm-caterpillar, *Euvanessa antiopa*, feeding on elm leaves. These are the larvae of the mourning cloak butterfly. These caterpillars are of the leaf-chewing type. (*University of Minnesota.*)

insects of this type: for instance, stands of ponderosa pine that have been defoliated by the pandora moth or the pine butterfly are frequently killed by bark beetles during the years following defoliation.

Types of Insect Defoliators.—Generally speaking, defoliating insects may be classified into three groups, according to their habits. Some species, called *leaf miners*, feed upon the succulent interior leaf tissues while tunneling between the upper and lower cuticula (Fig. 35). Others eat all the leaf except the vascular portions, thus skeletonizing the leaf, leaving only the veins

Fig. 58.—Mourning cloak butterfly, a species that attacks elms and willows in the larval stage. (*University of Minnesota.*)

(Fig. 56). These are called *skeletonizers*. Insects of the third group may be called the *leaf chewers* for they eat all the leaf tissues (Fig. 57). Some defoliators are miners during a part of their developmental period and skeletonizers at a later time. Others may be skeletonizers during their early stages and chewers during the later stages. But there are many species that belong to one only of these three classes during their entire developmental period. Regardless of the manner of their work, all the defoliators have essentially the same effect upon the life processes of the tree. The severity of the injury is directly proportional to the amount of chlorophyll-bearing tissues destroyed.

The most important tree-defoliating species are found in one of three orders: the Hymenoptera, the Coleoptera, or the Lepidoptera (Fig. 58), although there are a few members of other orders that feed upon the leaves of trees (Diptera and Orthoptera). Of the Hymenoptera, the family Tenthredinidae is typically a group of leaf eaters and contains many dangerous forest pests. Of the Coleoptera, the family Chrysomelidae is the most important group of defoliators. However, in some instances, members of the Scarabaeidae, for example, the may beetles, which are close relatives of the genus Melolontha of Europe, are very injurious. But of all the orders of insects the Lepidoptera is the one that contains by far the greatest number of leaf-eating species.

Space will not permit of even a brief discussion of all the tree defoliators known to science, in fact merely to mention the most important species would fill a volume; therefore, only a few typical examples of the different groups will be discussed here. At the end of this section there will be appended a list of some of the more important species that have not been taken up in this discussion.

LEPIDOPTEROUS LEAF EATERS

The members of the Lepidoptera are, on the whole, distinctly phytophagous, and by far the majority of species are leaf eaters. A discussion of a few members of this order will follow.

The Spruce Budworm.—One of the outstanding defoliators of fir and spruce in our Northern forests is the spruce budworm, *Cacoecia fumiferana* (Fig. 59). This is a native insect that is distributed throughout the range of its host trees. For years it may remain innocuous, a rare and inconspicuous resident of the forest, but when conditions are right it multiplies prolifically and is quickly transformed into a powerful forest devastator. Statistics given in Chap. I give some idea of the tremendous damage that this insect is capable of inflicting. The causes leading up to these outbreaks are not fully understood, but forest composition and the availability of an abundance of suitable food appear to be some of the important factors that make these outbreaks possible.

The life history of the spruce budworm exhibits a number of interesting features. The eggs are deposited during late summer in elongate clusters on the needles of the host trees. These

clusters are green in color and contain from 10 to 30 or more eggs. The eggs are flattened and overlap one another like shingles on a roof. The young larvae that soon hatch from these eggs seek out, without feeding, suitable places of concealment on the tree, spin a light covering of silk about themselves, and go into hibernation. The silken hibernating cases are called *hibernacula*. In the spring, about the time that the buds of the balsam fir are

FIG. 59.—The spruce budworm, *Cacoecia fumiferana*, adult moths, pupal skins, and larvae.

expanding, the larvae emerge from hibernation and begin feeding upon the fresh foliage of the host. As they work they web the needles together to form a crude shelter. The larvae develop rapidly and, under favorable conditions, in the course of three weeks are full grown.

During the first instars the larvae are a pale yellowish green with black heads and thoracic shields. Later, they become much darker until the general color is brown with black markings.

They then transform to the pupal stage on the trees. No true cocoon is spun, but the pupal stage is passed within the web spun about the tip by the larva while feeding. The adult moths emerge in July and early August, and soon thereafter they mate and deposit their eggs. The moths have a wingspread of nearly ¾ inch and vary in color from grey to copper. Two forms of this insect are found: one on fir and spruce, the other on pine. Those living on spruce or fir tend to be gray, whereas those reared on pine tend toward the copper shades.

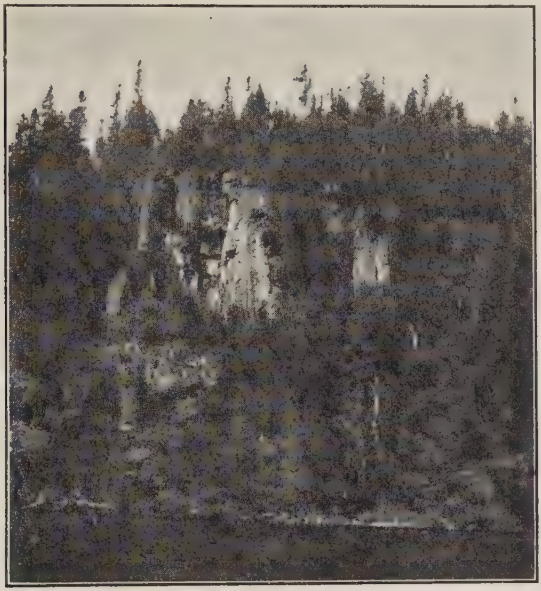


FIG. 60.—A Minnesota forest of balsam fir and spruce killed by the spruce budworm. (*L. W. Orr.*)

The development of the fir-spruce form of this pest is synchronized perfectly with the activities of the balsam fir. The larvae emerge from hibernation just in time to find on the balsam fir the fresh foliage that is required for their early development. The black-spruce buds open too late to supply much food for the larvae at this critical period. Even though the larvae burrow into the closed buds of black spruce in search of food, they are unable to find a sufficient supply for the needs of their first developmental stage. The white spruce, another host tree, pro-

duces abundant fresh foliage at the proper time, but the needles usually ripen up and become hard too quickly to permit full development of the budworms feeding upon them. Balsam-fir foliage, on the other hand, not only appears at the proper time but remains green and succulent during the entire period of larval development. In eastern Canada the red spruce appears to stand between the balsam fir and black spruce phenologically and also, as we would expect, in degree of susceptibility to budworm attack.

If these species of conifers were growing separately, it is probable that the budworm would be able to become epidemic only upon the balsam fir (Fig. 60). When, however, the balsam fir grows in combination with white, black, or red spruce, the larvae may, by migrating from one tree to another as food conditions require, find satisfactory conditions for development; in which case both the balsam fir and the spruce will suffer severely.

Thus in the Northeast, balsam fir is the favorite host of the spruce budworm, and without this desirable food plant it seems probable that extensive outbreaks, such as we have had in the past, would be impossible (Fig. 61). This gives us a clue to a practical and effective control measure and also explains, at least in part, the cause of the terrible outbreak of this pest that passed over our Northeastern forests during the decade between 1910 and 1920. Forest fires, logging operations, and natural succession in the latter part of the nineteenth century resulted in a decided change of forest type from pine and spruce to balsam fir, so that on vast areas, almost inconceivable in extent, balsam fir became the predominant tree. It was in these areas, predominantly pure fir, that the great outbreaks had their origin. The velocity of multiplication developed by the budworm in these favorable areas, because of the abundance of food and other favorable influences, doubtless made it possible for the insect to attack and kill other near-by forests where conditions were not so favorable for bud-worm development. It is probable that the forests containing a comparatively small proportion of balsam fir would have been safe from attack had it not been for the adjacent areas of pure or nearly pure balsam fir.

By controlling the composition of woodlands, future disastrous outbreaks of this pest in spruce-balsam forests can doubtless be prevented to a considerable extent. These silvicultural

procedures must be based on an understanding of the habits of the budworm, the ecological characteristics of the forests in which it occurs, and the economic demands in each particular case. The characteristics of the budworm have been considered, and at this point a brief discussion of the ecological and economic aspects will help to make clear how silvicultural procedures may result in the control of a forest insect.

On the one hand, balsam fir is a valuable tree which finds a ready market on a short rotation. It reproduces itself well and

FIG. 61.—A forest of douglas fir, in Yellowstone Park, defoliated by the spruce budworm. In the West this tree species is apparently comparable with the balsam fir of the East as a favored host of the budworm. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

grows rapidly. For these reasons, its elimination from the forest for the sake of budworm control is economically undesirable. On the other hand, both current logging practices and ecological succession tend to develop, in the budworm zone, forests that are predominantly balsam fir and that are certain ultimately to be attacked by the budworm.

It has been shown that young stands and stands in which the balsam is overtopped for the most part by other trees are not favorable to building up budworm outbreaks (Graham and Orr,

1939), and also that general outbreaks are always associated with extensive areas of susceptible forests. Furthermore, within the areas where budworm outbreaks are likely to occur, there is a sufficient number of tree species and diversity of forest types, so that the silviculturist can produce a great variety of conditions by appropriate manipulations.

By taking advantage of these facts, it is silviculturally possible to prevent the development of disastrous outbreaks of the budworm by preventing the development of budworm-susceptible types or, if this is economically undesirable, by preventing the development of susceptible stands on extensive areas at any one time.

A logical procedure would be to divide the stand into compartments not exceeding a section in area and preferably into 40-acre units. These units should be treated in a variety of ways so that there will be the maximum possible variation in age class and composition between the various adjacent units. Most of the units may ultimately reach a susceptible condition, but no contiguous areas should be permitted to reach this condition at the same time. Ideal conditions may be produced if thinnings, cleanings, planting, and other cultural procedures are economically feasible. In many instances, however, the regulation of logging operations may be the only practicable means of improving conditions. In this case, logging in 40-acre units and scattering the operations so that, in the next tree generation, units of the same age will be separated as far as possible from one another should result in a decided improvement of conditions.

The spruce budworm has, in the past, been regarded as a pest of fir and spruce alone. In recent years, however, this species has been observed attacking pines in epidemic numbers, both in the Lake states (Graham, 1935) and in the northern Rocky Mountain Region (Balch, 1930). From preliminary experiments in the Lake states, it appears probable that the budworm on pine, although identical specifically with the spruce-fir form, is a distinct biologic race or variety. For although it is possible for the larvae to continue development and reach maturity successfully after being transferred from spruce or balsam to pine, and vice versa, there appears to be little migration of this sort in nature. The balsam fir and spruce in the region where the jack pine is infested by this pest remained untouched even though

they were close to infested jack pine. Likewise, the pest did not migrate from the balsam-spruce forests that were killed by it into the adjacent stands of jack pine. This evidence lends substantial support to the conclusion that the budworm on pine is biologically distinct from the balsam-fir form.

If it is true that the insects do not change readily from pine to other hosts, or vice versa, then each of the two forms may safely be treated from the economic aspect as if it were an individual species, with the result that the problem of control will be much more simple to handle than if the budworm could easily change from one host to another. Studies indicate that the budworm on pine, like the fir-spruce form, may be controlled by silvicultural procedures, but these procedures are very different from those previously described. On jack pine, the young larvae thrive best when they feed on pollen during the early stages. Unless this food is present in abundance, they seldom, if ever, become seriously epidemic. An abundance of staminate flowers is most frequently found on trees with large crowns, growing in scattered stands, or on overmature round-topped trees. Presumably this is because the carbon-mineral ratio in such trees is especially favorable for flower production, particularly during periods of rainfall deficiency when outbreaks of the budworm are most common.

By growing jack pine in fully stocked stands, by eliminating jack-pine wolf trees from pine plantations, and by utilizing the trees before they become overmature, budworm outbreaks on jack pine may be controlled.

On ornamental trees it is profitable to use the direct methods of control. These methods are expensive, but certain, and where valuable individual trees are to be protected, they may be applied with profit. Spraying or dusting of infested trees with lead arsenate or calcium arsenate at the time the buds are expanding is an effective means of destroying the larvae of this insect. In dusting, the powdered form of these insecticides may be used either pure or may be diluted with fine, air-slaked lime. When a liquid spray is used, the poison should be mixed with water at the rate of 3 to 6 pounds of the powder to 50 gallons of water.

The Gypsy Moth.—The gypsy moth, *Porthetria dispar*, is one of the many destructive insect pests that has come to America from foreign lands (Fig. 62). This pest was accidentally intro-

duced at Medford, Mass., in 1869, and since that time it has spread into all the New England states. It is particularly injuri-

FIG. 62.—Stages of the gypsy moth. The large light-colored moth is the female. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

ous to broad-leaved trees, although pines in mixture with hardwoods are by no means immune.

The eggs are laid during July in clusters of 400 or more. Since the heavy-bodied female moth is unable to fly, the eggs are usually deposited near and often on the cocoon. The eggs pass through the winter, not hatching until the following spring. The larvae feed in the first stage upon the foliage of susceptible trees such as oak, basswood, and aspens, and later they may also

FIG. 63.—An oak forest in Massachusetts killed by gypsy-moth defoliation. Oak is one of the species most susceptible to gypsy-moth attack. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

feed upon chestnut, hemlock, pine, and spruce. If the infestation is severe, the trees may be completely defoliated by the end of June (Fig. 63). When full grown, the larvae pupate, either on the tree or in other convenient places, and after a pupal period of about 10 days, the adults emerge. The male moth is brown in color, whereas the female is white with black markings. Unlike the female, the male is a good flier.

At first thought, it would appear that a species whose adult females were unable to fly would have little chance of spreading from one locality to another, and would, consequently, be confined to a restricted area and there very easily be controlled. This has not, unfortunately, proved to be the case with this pest. One of the important means of distribution for the gypsy moth is wind. The first-stage larvae are clothed with long hairs which greatly increase the surface area of the body in proportion to its weight. The larvae at this stage are so light that they can be carried long distances by air currents. How far they can be blown in this way can only be a matter of conjecture, but it is known that they have been carried over water for a distance of more than 20 miles. That this is one of the important means of gypsy-moth dispersal is indicated by the fact that the most rapid spread of the pest has been in the direction of the prevailing winds. Other means of dispersal are of a more or less accidental character; for example, egg masses or larvae may be carried on persons or vehicles leaving the infested area.

The effect of climatic factors upon the gypsy moth is of great importance both directly and indirectly. A temperature of −20°F. is sufficient to kill the overwintering eggs, and, as a result, in severe winters only those eggs that are beneath the snow line, or in other protected locations, survive. This, of course, has an important effect upon the abundance of the species during the following season. Cool, moist conditions followed by warm weather during early June are favorable to the development of the wilt disease which is an important natural check of this moth.

Parasites and predators of the gypsy moth have been introduced into the infested area and are, each year, becoming more and more effective, but are still far from giving adequate control. In fact, neither parasites nor predators can be expected to give perfect control. Under present conditions, the best that can be hoped for is to bring about a condition similar to that which obtains in the native home of the pest where the parasites help to prevent outbreaks but do not, by any means, prevent them altogether.

Because of the differences in susceptibility of various tree species, the regulation of forest composition by the application of silvicultural principles promises to be the most effective method

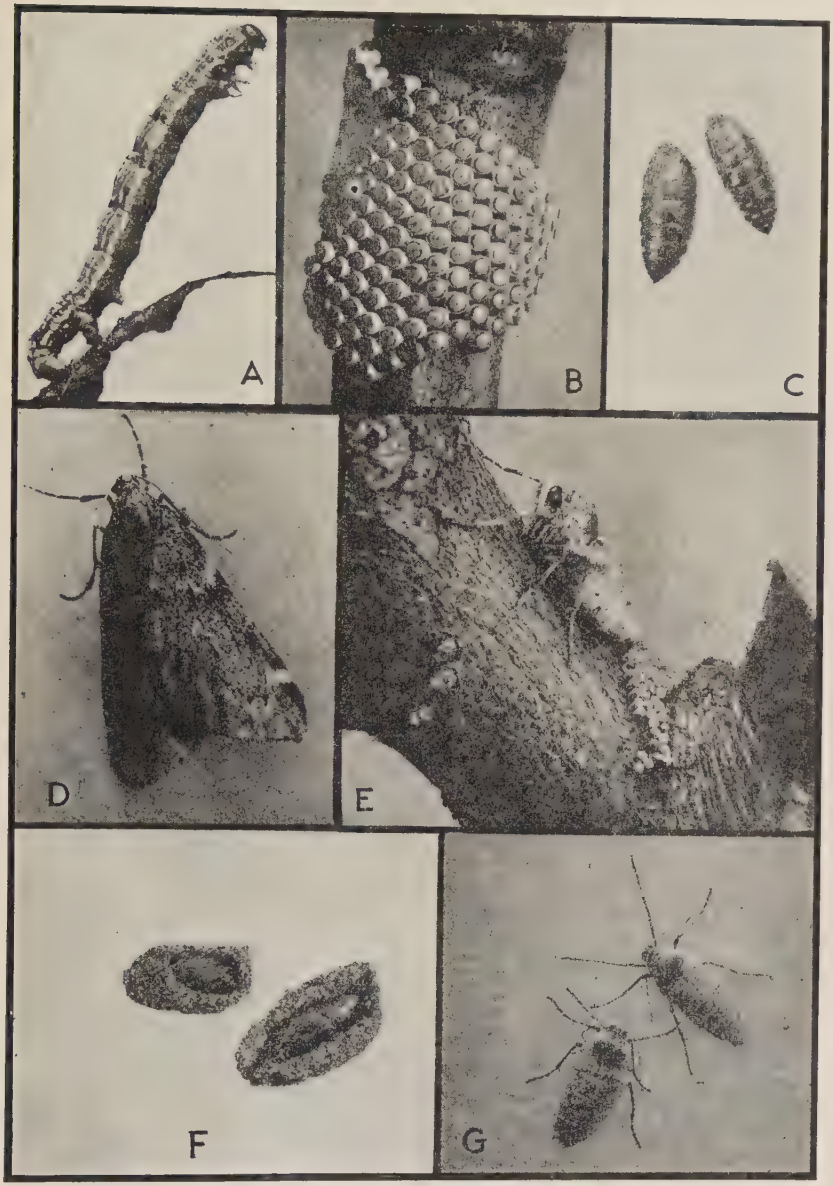


FIG. 64.—The fall cankerworm, *Alsophila pomentaria*. *A*. Full grown larva. *B*. Cluster of eggs. *C*. Pupae. *D*. Adult male. *E*. Adult female in act of oviposition. *F*. Pupae in cocoons. *G*. Adult females. Note the absence of wings. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

of protecting forests from the gypsy moth (Behre, 1936). By eliminating the most susceptible species, a forest may be made comparatively safe. Much further work along this line is necessary before completely satisfactory methods can be developed.

Ornamental and shade trees may be protected effectively by the application of direct control. Spraying with lead arsenate at the rate of 3 to 6 pounds of the powder to 50 gallons of water is effective. In connection with this work, powerful spraying machines and special nozzles designed to throw a spray to the tops of tall trees have been perfected. The use of sticky bands

Stage	Spring cankerworm	Fall cankerworm
Egg	Dull grey, oval, in sheltered locations in irregular groups on trunks and branches	Grey, flowerpot-shaped, deposited in regular clusters on trunks and branches
Larva	Yellowish brown to black in color, only 2 pairs of prolegs	Striped with white and yellow on black, three pairs of prolegs
Pupa	No cocoon spun	Tough, silken cocoon
Adult	Abdominal segments with double transverse rows of reddish spines	Abdomen without spines

has been found useful in preventing larvae from creeping up the trunks of uninfested trees. Burlap bands under which the larvae may congregate during the day are also useful in controlling this pest. The caterpillars that collect beneath these bands can easily be killed, mechanically, by crushing them.

The Cankerworms.—Two species of measuring worms, known as the fall cankerworm, *Alsophila pomentaria*, and the spring cankerworm, *Paleacrita vernata*, become periodically epidemic throughout the greater part of the Eastern hardwood-forest region as far south as the Carolinas and Tennessee. They also occur in California. These species are similar in appearance, and frequently the larvae are found working together on the same trees. The favorite host trees of these worms are the elms and the basswood, although they also attack a wide variety of other hardwood species (Fig. 64).

Although these two species look very much alike superficially, on closer examination they are seen to be really different in every

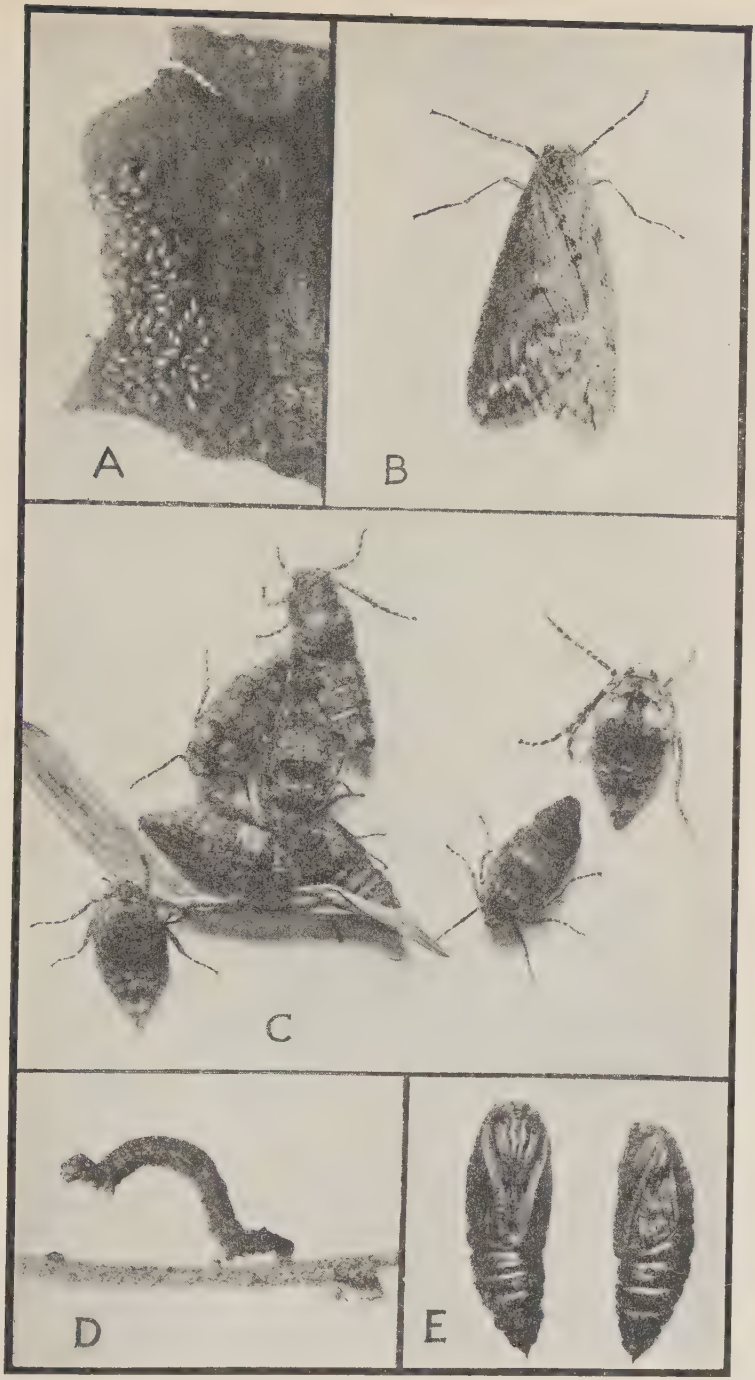


FIG. 65.—The spring cankerworm, *Paleacrita vernata*. *A*. Mass of eggs on the bark of a tree. *B*. Adult male. *C*. Adult female moths. *D*. Full grown larva. *E*. Pupae. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

stage (Fig. 65). For convenience the most obvious distinguishing characteristics are summarized in the table on page 180.

The eggs of the fall cankerworm are laid late in the autumn, usually after freezing weather has occurred, whereas the spring species oviposits very early in the spring. The female moths of both species are wingless and crawl up the trees from the ground, where they have pupated, to oviposit in the tree tops. The larvae of both hatch in the spring and feed upon the expanding foliage. Four to five weeks are required to complete the larval

FIG. 66.—The pandora moth, *Coloradia pandora*. Adult male. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

feeding period. When full grown, the larvae drop to the ground and transform to the pupal stage. The fall species spins a tough silken cocoon about itself before pupating, but the spring species passes through the pupal period without this protective covering.

These insects have been little studied as forest pests; therefore no control measures have been developed that are applicable under forest conditions. On shade and orchard trees, either banding with sticky bands, to prevent the wingless females from climbing into the tree tops for oviposition, or spraying with arsenicals is effective. Under natural conditions, these species are held in check by parasites and predators, of which birds are probably the most important single factor. Certain weather conditions, such as cold, wet weather shortly after the larvae have hatched from the eggs, or damp weather followed by high temperature, are unfavorable.

The Pandora Moth.—An important defoliator of ponderosa and Jeffrey pine throughout the West but especially in southern

Oregon and California is the pandora moth, *Coloradia pandora* (Fig. 66). This large gray moth (Patterson, 1929) becomes periodically epidemic at intervals of about 20 years, and severely defoliates its host tree. The effects of this defoliation are twofold,

FIG. 67.—Pandora-moth defoliation of ponderosa pine. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

direct and indirect. The direct effect is a marked reduction in growth rate of the injured trees, which in an outbreak in southern Oregon, according to Patterson, amounted to several hundred thousand dollars. Trees are not usually killed by the defoliation. The indirect effect is the marked increase in bark-beetle damage that almost invariably follows an outbreak of the

pandora moth. Following the outbreak mentioned by Patterson, the loss in a single year on the Klamath Indian Reservation amounted to nearly 100,000,000 feet b.m. (Fig. 67).

The Indians in the West find the pandora moth a much appreciated source of food during the periods of its abundance. The Klamath and Modoc Indians formerly collected the pupae from the soil and prepared them for consumption by roasting (Patterson, 1929). The Piute Indians, according to Miller (1928), collect the larvae by trapping them in trenches as they crawl

FIG. 68.—Dried larvae of the pandora moth, "peaggie," used for food by the Piute Indians. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

from the trees to pupate. These larvae are roasted in mounds of earth, heated by fire, and then dried in the shade. These dried caterpillars they call *peaggie*. They are eaten as a stew with vegetables (Fig. 68).

The pandora moth has an unusually long life cycle for a lepidopterous insect. It requires 2 full years for its completion. The adults appear in June and July and lay their eggs in groups on the bark or needles. The eggs hatch during July and August, and the young larvae feed more or less gregariously upon the current year's needles. Cold weather forces them into a condition of hibernation among the clusters of needles near the end of the branches. In the following spring, they scatter over the tree feeding on both old and new foliage until they become full grown in the latter part of June. They then crawl to the ground, where they pupate, until the following July. Thus, during an outbreak, the trees are severely defoliated only in alternate years, during the spring feeding period, when the larvae are large and

extremely voracious. This characteristic probably accounts for the relatively small number of trees killed directly (Fig. 69).

Patterson suggests the use of stomach insecticides for the control of this insect. Because of the high value of the trees attacked and the relative ease with which the larvae could be poisoned, this seems to be economically feasible. The method

Fig. 69.—The pandora moth, *Coloradia pandora*, caterpillars feeding. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

has not been tested, however, under practical conditions. It would appear that the application of an arsenical spray from an autogiro might be the most effective and economically feasible method of control.

It seems doubtful if silvicultural methods can be developed immediately for the control of this insect, although this possibility should not be overlooked in future tree generations.

Other Lepidopterous Defoliators.—Although space will not permit consideration of the numerous other species of Lepidoptera

that may seriously injure forest trees, there are a few others that should be at least mentioned here. The pine-tube moth, *Eulia* (*Argyrotaenia*) *pinatubana*, has caused serious injury to lodgepole pine in Idaho and Wyoming (Burke, 1932). This is a tortricid moth that ties the needles of the new growth together and feeds within the clusters of tied needles. It is especially injurious when it attacks the trees in combination with the lodgepole sawfly, *Neodiprion burkei*, which confines its feeding to the old needles.

The tube moth is widely distributed both in the East and West, but its habits vary locally. For this reason, Burke suspects that there may be more than one species, although only one is recognized by taxonomists. One of the variations in habit is in pupation. In the East, the pupa occurs on the trees within the tubes, whereas in the West, cocoons are spun in the litter beneath the trees.

Burke suggests that this insect be controlled by spraying with an arsenical. The effectiveness of this method has been demonstrated, but the cost of spraying from the ground varied from $6.50 to $10.00 per acre, an expenditure that cannot be justified, except under very special circumstances. Spraying from the air would doubtless be cheaper. Burke also suggests the possibility of light burning to destroy the pupae as they lie near the surface of the litter beneath the trees, but points out the extreme difficulty of controlling the fire so as to obtain the proper degree of burning without causing injury to the forest.

Another insect that seriously defoliates lodgepole pine in California at high elevations is the lodgepole needle-miner, *Recurvaria milleri* (Patterson, 1921) (Fig. 70). The secondary effects of this insect's attack are more serious than the direct defoliation, because the weakened trees, which otherwise would recover, are usually attacked and killed by *Dendroctonus monticolae*. This insect has a 2-year life cycle. Oviposition occurs in August and September, after which the larvae mine the needles and pass the winter in them. They continue to mine these needles until the following August, when they move to the current needles of that year, in which they mine, pass the second winter, and pupate during the following June and July. They emerge as moths in the following July and August. Patterson suggests that silvicultural procedures designed to convert the high-elevation

lodgepole types attacked by the needle miner to fir and mountain hemlock would be a desirable procedure.

Still other lepidopterous defoliators that should be mentioned are: The European larch-casebearer, *Coleophora laricella*, an introduced enemy of larch (Britton, 1924; Felt, 1933) that is important on tamarack; the satin moth, *Stilpnotia salicis*, an enemy of willow and poplars that has found its way from Europe

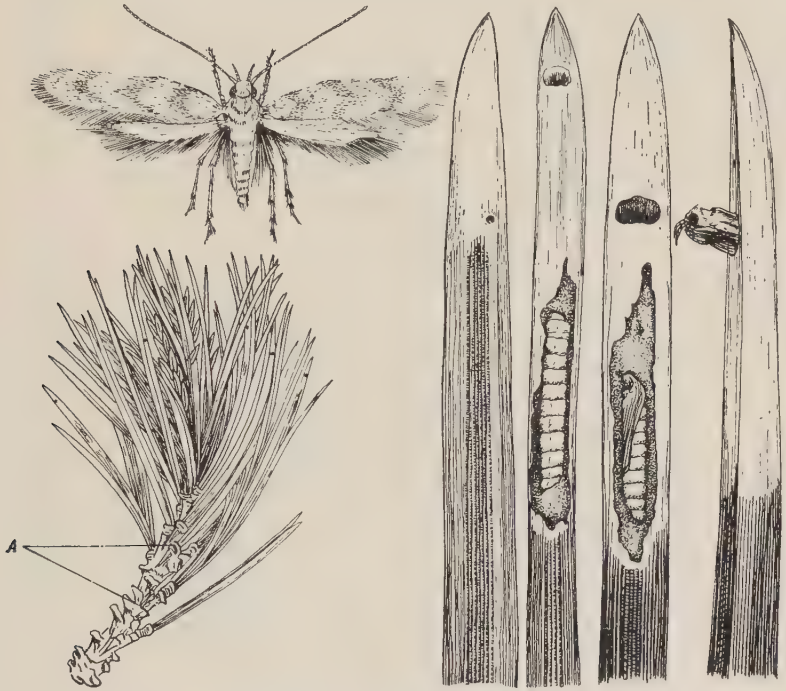


FIG. 70.—Lodgepole needle-miner, *Recurvaria milleri*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

into both the East and West (Collins, 1931); the douglas-fir tussock-moth, *Hemerocampa pseudotsugata* (Keen, 1938), that is periodically epidemic on douglas fir; the hemlock looper, *Ellopia fiscellaria* (Fig. 78), and its western variety, *lugubrosa*, that have caused disastrous defoliation of hemlock both in the East and West (Hopping, 1934); the forest tent-caterpillar (Fig. 75); its close relative the Great Basin tent-caterpillar (Fig. 80); and the pine butterfly, *Neophasia menapia*, which occasionally becomes

epidemic on western white-pine (Evenden, 1926) (Figs. 76, 77). References to still other species will be found in the bibliography.

COLEOPTEROUS LEAF EATERS

The leaf-eating insects that belong to the order Coleoptera are almost all members of a single family, the Chrysomelidae, although the members of the genus Phyllophaga (Lachnosterna)

FIG. 71.—The elm leaf-beetle, *Galerucella xanthomelaena*. 1. A cluster of eggs 2 and 3. Larvae. 4. A pupa. 5 and 6. Two adults illustrating the light and dark color forms. 7. Larvae feeding on a leaf. 8. A leaf skeletonized by larval feeding. 9. A leaf showing holes made by the adult beetles in feeding. (*Felt*, "*Manual of Tree and Shrub Insects.*")

of the family Scarabaeidae are defoliators in the adult stage. Only a few of them are important forest or shade-tree pests, and very little space can be allowed them here.

The Elm Leaf-beetle.—The elm leaf-beetle, *Galerucella xanthomelaena*, is another of our introduced pests. It first appeared in Baltimore, Md., about 1834, and since that time has established

itself throughout the Middle Atlantic and New England states, and westward into Ohio, Indiana, Michigan, and Kentucky, and more recently Oregon and California. It is primarily a pest of shade trees and has not as yet become an important factor in the forest (Fig. 71).

Fig. 72.—An adult poplar leaf-beetle. (*University of Minnesota.*)

The winter is passed in the adult stage. After emerging from hibernation the beetles feed for a time on the expanding leaves of elm trees, and there they later deposit their yellow eggs in clusters of from 5 to 25. The larval feeding period lasts from 2 to 3 weeks.

When they are full grown the larvae transform to the pupal stage on the ground, or in secluded places on or near the trees, where they have been working. The adults emerge in from 6 to 10 days, thus completing the life cycle. There may be two, and possibly more, generations per year, depending upon the length of the season.

Fig. 73.—Adult larch sawfly ready to oviposit in a young larch shoot.

Spraying or dusting shade trees with an arsenical at the rate of from 5 to 8 pounds per 100 gallons of water is the most effective method of controlling this beetle.

The Poplar Leaf-beetle.—The poplar leaf-beetle, *Chrysomela scripta*, is a serious pest in basket-willow plantations and occasionally is injurious in aspen forests (Fig. 72). With the rapid increase in the area of our poplar forests, and the favorable food conditions resulting therefrom, there is an ever-increasing danger of an epidemic of either this insect or the closely related species *Chrysomela interrupta*.

The adult poplar leaf-beetle varies in size but is usually from $\frac{3}{16}$ to $\frac{1}{4}$ inch in length. The background color is yellow, and the markings are elongate black spots and lines. The insect passes the winter in the adult stage. In the spring, the beetles emerge from hibernation and, after a brief period of feeding, deposit their eggs in clusters on the underside of the leaves. The larvae,

after hatching, feed upon the foliage gregariously. They are dark-colored, flattened grubs with well-developed legs and tapering abdomens. First they skeletonize the leaves, and later they eat irregular holes between the principal veins. When they are full grown, the larvae drop to the ground and there pupate. The length of the developmental period varies with the temperature to which the insects are exposed. It is said that only 15 days are required under favorable conditions. The number of generations varies in different localities, according to the climatic conditions, but usually there are two in the Northern states. This beetle is generally distributed throughout North America wherever its host plants are found.

In plantations of basket willow and on ornamental trees, the poplar leaf-beetle may be effectively controlled by stomach poisons applied in the form of either a spray or a dust.

HYMENOPTEROUS LEAF EATERS

By far the greater proportion of all the leaf-eating Hymenoptera belong to the family Tenthridinidae. The adults of this family are called *sawflies* because of the saw-like ovipositor of the female. The larvae are, for the most part, very similar to the caterpillars of the Lepidoptera in general appearance and are sometimes called *false caterpillars*. Most of the common species may be distinguished from the true caterpillars by the presence of at least six pairs of prolegs on the abdomen. Several important defoliators of coniferous and broad-leaved trees are members of this group. One of the most outstanding of these is the larch sawfly.

The Larch Sawfly.—One of the most serious defoliators of larch, in both Europe and America, is the larch sawfly, *Pristiphora erichsonii*. In America, this pest was first reported in New England, in the early eighties, where it was responsible for much damage to the native larch. Since this early outbreak the species has played a prominent part in defoliating larch.

Packard and Felt assume that it is one of our uninvited guests, and that it was introduced into America prior to 1880. Hopkins, on the other hand, maintains that it is a native of America. The facts that it remained unknown in this country until 1880 and also that the outbreak appeared to spread gradually westward from the Atlantic seaboard, are evidence in support of the former

view. A study of the annual rings of old living tamaracks, however, show that this tree has presumably suffered repeatedly from defoliation injury. It is not unreasonable to assume that this injury was very likely due to the sawfly. In Minnesota, the first historical record of larch-sawfly injury is in the year 1909. The ring pictures of old trees, however, show that reduction from defoliation has occurred periodically throughout the life of the oldest trees. In addition to the recent period of reduced growth that started about 1909, there were at least two other periods of heavy defoliation, one just previous to 1880 and another about 1840. Other minor defoliations occurred about 1855 or 1860, about 1870, and in the late nineties. Whether or not the larch sawfly is a native or an introduced pest can be shown only by further and more extensive studies.

The life cycle of the larch sawfly is quite similar to that of many other sawflies. The eggs are deposited in the young shoots during the period of rapid spring growth. When first deposited they are translucent and very small. They soon swell, however, as a result of adsorption of water until they protrude from the slit in which they are placed. They are deposited alternately in a double row of slits cut along one side of a rapidly expanding fresh shoot. The oviposition injury usually results in killing one side of the shoot, while the other side continues to grow. This type of injury results in a marked twisting of the injured tips. The abundance of these twisted twigs can be used as an index of sawfly abundance in a stand.

The eggs hatch in about a week and the larvae begin devouring the foliage. They are pale green in color, with black heads. They usually work gregariously, and, as a rule, they completely defoliate one branch before moving to another. Full growth is reached by midsummer, when the larvae drop to the ground and spin their tough, brown, oval cocoons in the moss or litter beneath the trees. The larvae remain in the prepupal stage within these cocoons until the following spring when the majority of them transform to the pupal stage and emerge as adults. The remainder hold over in the prepupal stage until the second spring after cocooning, when they, too, transform to the adult stage. The adult sawfly is a handsome black insect somewhat over $\frac{3}{8}$ inch in length, with a bright orange band about the base of the abdomen (Fig. 73).

On shade and ornamental trees a spray or dust of lead arsenate or calcium arsenate is an economical and effective control measure. In the forest no effective means of holding this pest in check has, up to the present, been found. It has been shown, however, that thrifty, rapidly growing trees are much better able to recover from the effects of defoliation than less thrifty trees. This suggests that light surface drainage, to remove the surplus water from the tamarack swamps, would probably be beneficial in increasing the resistance of the trees. Recent experiments indicate the possibility that superficial drainage may so change the character of the ground cover, beneath the trees, that conditions may be made less favorable for sawfly hibernation than in undrained swamps.

FIG. 74.—The jack-pine sawfly, *Neodiprion banksianae*. Adult female and male. The female is the larger of the two.

The Pine Sawflies.—Several species of sawflies are injurious defoliators of pine. Some, like the jack-pine sawfly, *Neodiprion banksianae* (Fig. 74), attack the older trees, while others, of which *Neodiprion lecontii* is a good example, prefer to attack the younger trees.

All the members of this group deposit their eggs in slits cut in the edge of living pine needles. Some species pass the winter in the egg stage and the young larvae hatch out in the spring; in other cases, the winter is passed in the prepupal stage within the cocoon. Most species like *Neodiprion banksianae* have a divided emergence similar to that of the larch sawfly. That is, a part of the adults emerge in the fall following cocooning, while a part of them remain for a year longer within the cocoon. This protects the species against such seasonal catastrophes as may arise directly or indirectly from adverse weather conditions. The jack-pine sawfly appears to be one of the most dangerous

of the sawfly defoliators of pine and, during recent years, has been responsible for considerable injury in certain large areas in the Lake states. The adults of this species appear in the autumn. The sexes are so different in appearance that it might easily be thought that they were different species. The males are only about ¼ inch in length, much smaller than the females, black in color, with feather-like antennae. The females are almost ⅜ inch in length, yellowish brown in color, and the antennae are thread-like.

The winter is passed in the egg stage in the needles on the host tree. The eggs hatch during May, and the larvae complete their development in a very few weeks. Even under cool conditions, the length of the larval period does not usually exceed 5 weeks, and under favorable conditions this period may be much shortened. In the early instars, the larvae are a uniform green color with black heads. In the third instar, black longitudinal stripes begin to appear, which become very strongly marked in the full grown larva. There is but one generation per year. The cocoons are spun in the litter on the ground beneath the infested trees. The larvae remain in the prepupal stage until late August or September, at which time a part of them transform to pupae and later to adults, while the others remain in the prepupal stage until the following August or September.

Food conditions for this sawfly are much more favorable than they were 20 or 30 years ago. In fact, it is evident that they are ideal when the large areas, formerly covered with red and white pine, that are now occupied by jack pine are considered. Parasites are abundant but do not occur in sufficient numbers to hold the pest in check. Apparently, under present conditions, the most important factors that regulate the abundance of this sawfly are the weather factors. Heavy rains during the larval stage, or cool moist weather followed by hot weather, checked threatened epidemics during the seasons of 1924 and 1925, either by washing the larvae from the trees or by making possible the development of a wilt-like disease. In 1926, an early spring followed by late frosts killed many larvae, thus reducing the numbers of this insect. In spite of these controlling influences, enough adults have emerged each of these years to provide an abundant supply of eggs for the next season. Under favorable weather conditions, therefore, which means warm dry weather during May and early

June, an outbreak of this pest in large areas in Minnesota may be expected.

The control of this pest in forests has not been adequately investigated, but it appears that the situation would be ameliorated by a reduction in the area occupied by jack-pine forests, and a return to the better balanced mixed-pine forest. Ornamental trees may be effectively protected against this pest by spraying or dusting with an arsenical while the insects are in the larval

FIG. 75.—Larvae of the forest tent-caterpillar. Note the line of light-colored spots that serve to distinguish this caterpillar from other closely related species. (*University of Minnesota.*)

stage. It is desirable to apply the poison while the larvae are still small, because they are much more susceptible at that time, and, moreover, if treatment is delayed too long, an unnecessary amount of defoliation will occur before they are killed.

The European Spruce Sawfly.—The European spruce sawfly, *Diprion polytomum*, was discovered in the Gaspé Peninsula in Canada in 1930. How or when it reached this side of the Atlantic from its native home in Europe is not known (Balch, 1934, 1936, and 1938). Since its discovery, it has virtually destroyed the stands of mature spruce in the Gaspé Peninsula

and in other places in Canada and in parts of New England. It is now known to be established as far west as Guelph, Ont., and

FIG. 76.—Adults of the pine butterfly. (*F. P. Keen.*)

FIG. 77.—Defoliation of yellow pine by the pine butterfly at New Meadows, Idaho. (*J. C. Evenden.*)

may soon be expected to reach the stands of spruce in the Lake Superior region.

The adult sawfly is about $\frac{3}{8}$ inch in length, thick-waisted, and, like the other members of this family, provided with a saw-like ovipositor. In color it is black with yellow markings on the abdomen, thorax, and head. It is a parthenogenetic species, and males are seldom found. This, of course, adds materially to its potentialities for reproduction.

According to Balch, the adult females emerge in the spring from the oval, brown cocoons that were spun by the larvae in the

FIG. 78.—Adult moths of the hemlock looper, *Ellopia fiscellaria*. (*A. A. Granovsky.*)

duff layer beneath the trees. They lay their eggs in slits cut in the needles with the ovipositor. The larvae that hatch from these eggs pass through six instars, during the first three of which they are a pale green in color. During the fourth and fifth instars, they become striped with five longitudinal white stripes that again disappear in the sixth and final instar.

The eggs are laid in the old needles of all species of spruce. White spruce is especially favored. On hatching, the larvae feed on the old needles until the current year's needles are mature, after which some feeding may occur on them. They are not

gregarious, like so many sawflies, but feed singly at first, chewing notches in the needles and later consuming the entire needle. This feeding habit makes their injury inconspicuous until it has reached serious proportions. Their presence is indicated by a

FIG. 79.—Larvae of the hemlock looper feeding upon hemlock needles. (*A. A. Granovsky.*)

thin appearance of the foliage and the presence of frass dropped by the caterpillars under the trees.

In the Gaspé Peninsula, only one generation occurs, but in parts of New England, as many as three may be completed (Peirson, 1936). When full grown, the larvae drop to the ground and spin their cocoons in the duff above the mineral soil. Some of the overwintering larvae may lie dormant in the cocoon for several years, but most of them will transform to pupae and adults the spring following cocooning.

It is too early to predict the future status of this insect in its new environment. Some authorities are convinced that it may exceed in injuriousness the spruce budworm. It was free from parasites when first discovered in Canada, and its only natural enemies were birds, mice, voles, and shrews. In some places, these animals destroyed a large proportion of the cocoons, but not a sufficiently large number to control the insect.

Parasites have been and are being introduced from Europe, and it is hoped that these natural enemies will be able to check this outbreak and hold the insect within bounds. No other control in the forest has been recommended. On shade trees, the usual spraying procedure, using lead or calcium arsenate, is effective.

In the preceding discussion of defoliation and defoliators only a few specific insects have been considered. These will serve to illustrate the general type of injury, and some of the methods of control that may be used in combating insects of this type. Many other species might have been used equally well as illustrations, and if space permitted they might have been discussed to good advantage. Some of these are the forest tent-caterpillar (Fig. 75), the fall webworm, the white-marked tussock-moth, the pine butterfly (Figs. 76, 77), and the hemlock looper (Figs. 78, 79). For the benefit of those who may wish to study these and other defoliators a list of reading references is given under Leaf-eating Insects in the general bibliography.

CHAPTER XI

MERISTEM INSECTS OF THE TERMINAL PARTS

The meristematic tissues, as compared with other portions of a tree, are high in protein content and are, therefore, among the parts held in favor by many insect species. In number of species, the meristem eaters are exceeded only by the leaf eaters. The term *meristematic tissue* is here interpreted to include not only the cambium layer proper and the growing tips, but also the adjacent soft portion of the xylem and phloem.

GROUPS OF MERISTEM INSECTS

In a discussion of insects feeding upon the meristematic tissues, we may classify them on the basis of their taxonomic position, or on the basis of the condition of their host, or on the basis of the part of the tree on which they feed.

On Basis of Taxonomic Position.—Among the meristem insects are found representatives of several orders. Among the Diptera there are a number of cambium miners that find their nourishment in living trees. These dipterous miners do not kill trees and are, consequently, of comparatively little economic importance. It is said, however, that their activities are responsible for certain minor defects of birch and maple, called *pith flecks*. Some of the Chironomidae, called *pitch midges*, feed upon the cambium and phloem of coniferous trees (Fig. 81). The pitch that exudes from the tree covers the larvae and serves as a protection for them. Although numerous, this group contains no dangerously injurious species. There are also numerous dipterous species that inhabit the cambium and phloem region of dead trees or logs without being true meristem eaters. They either feed upon microorganisms, like fungi, that are found in these locations, or, as in the case of the snipe flies, they are predaceous upon the true meristem eaters. Thus the Diptera found in meristematic tissues cannot be regarded from the economic aspect as a very important group.

Among the Lepidoptera, on the other hand, are many important meristem insects. Certain species of the family Aegeriidae, for example, the clear-winged moths, feed upon the meristematic tissues of the trunk and branches of trees. Some of them that

FIG. 80.—Work of Great Basin tent-caterpillar on bitter brush, a valuable range plant in Western forests. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

attack conifers are known as *pitch moths* because of the mass of pitch which exudes from the injured tissues. When such injuries become overgrown by wood, pitch pockets are formed. These defects, when numerous, materially reduce the merchantable value of the lumber produced from the trees. The superfamily

Tortricoidea of the Lepidoptera also contains a number of typical meristem insects. The tipmoths and bud miners furnish many illustrations of this group.

But of all the meristem insects those that feed on the cambium and adjacent soft tissues of the xylem and phloem are by far the most important group. In the past these insects have usually been called *cambium insects*, but obviously their activities extend beyond the thin cambium layer. Because most of their tunneling is in the phloem, current usage tends toward the name *phloem insects* for this group. This term has, therefore been adopted for use in this text. Of the phloem insects the larger proportion belongs to the order Coleoptera. The families of beetles that most commonly feed upon phloem are the Curculionidae, the Scolytidae, the Cerambycidae, and the Buprestidae. Each of these families contains species that are highly specialized for life in that region, and many of them spend their entire development period there. Others require the succulent and nourishing tissues only during the early developmental stages, and later are able to obtain nourishment in the solid wood to complete their development. All the various types will be included in this discussion.

FIG. 81.—A pitch mass on pitch pine caused by the work of the pitch midge.

In a brief review of meristematic insects such as this must be, only a few species can be selected for discussion. A supplementary list of some other species belonging to this group, with reading references, will be appended in the bibliography, for the convenience of those who wish to expand their study of these insects.

On Basis of Host Condition.—Meristem insects are often referred to as being either *primary* or *secondary* in character. These are exceedingly convenient terms. Unfortunately, they have been used rather loosely in forest entomological work, and therefore it is important that the sense in which these terms are used herein be made clear. A primary insect is an insect that is able to attack a healthy, living tree and complete its normal

development therein. A secondary insect is one that is incapable of attacking and completing normal development in a healthy tree. It would be possible to classify meristem insects on this basis, but in this discussion another arrangement seems more desirable. The terms primary and secondary will, however, be used as defined above in connection with certain species.

On the Basis of Feeding Place.—For the purposes of discussion, it is more convenient to classify the meristem insects into three main arbitrary groups based upon the part of the tree affected. These divisions are as follows:

1. Insects feeding on the terminal parts of trees.
   a. On twigs, tips, or shoots.
   b. On small roots.
2. Insects confined to the phloem region of the trunk and branches.
3. Insects attacking both phloem and wood.

The remainder of this chapter will be devoted to a discussion of some of the various meristem insects that feed on the terminal parts of trees, dividing them into two minor groups on the basis of whether the terminal part attacked is above or below ground. The other two chief groups will be discussed in the two following chapters.

INSECTS FEEDING ON THE TIPS

This group contains a multitude of insect species but, fortunately, only a comparatively small number of them are sufficiently abundant to be classed as serious pests. The members of this group seldom kill the trees that they attack. Their chief effect is to either reduce the rate of terminal growth or cause deformities that reduce the merchantable value of timber. In some cases they cause a reduction in both growth and quality. An exception to the rule that these insects seldom kill trees is found in cases where these tip destroyers attack seedling or sapling trees. In such instances they frequently kill the little trees.

The Nantucket Pine-moth.—One of the truly injurious tip feeders is the Nantucket pine-moth (pine tipmoth), *Rhyacionia* (*Evetria*) *frustrana*. This species was first reported from Nantucket Island, by Scudder in 1876, where it was said to be killing pines 20 to 30 years old. A few years later Comstock reported it

as being abundant upon Virginia scrub pine near Washington, D. C. Since that time it has been found that this species, including the closely related western variety known as *Rhyacionia frustrana bushnelli*, is generally distributed throughout the pine forests of North America and is responsible for an immense amount of damage to small pines, both in natural reproduction and in plantations. In the East, this insect has not attracted much attention, since the outbreak on Nantucket Island in 1876, until recently. In 1925 another serious outbreak was reported from Cape Cod. During the intervening period the species has been present and has reduced the growth of small trees in the East, but it has not been sufficiently abundant to kill trees.

The western variety has, in some places, done very little damage, while in other localities it has been very injurious, especially to ponderosa-pine seedlings and small saplings. In the Lake states and the Black Hills, the Nantucket pine-moth can be found in practically every stand of young pine but is never an injurious insect. In the sand-hill plantations of the Nebraska National Forest and farther south, on the other hand, this insect has proved to be a most serious pest.

The number of generations per season varies with latitude. Only one generation occurs in the Lake states and the Black Hills, but in the South there may be three or, possibly, four. In the latitude of Nebraska there are two generations. This variation is, doubtless, one reason for the difference in economic importance of this species in different localities. In the Lake states and the Black Hills, where there is only one generation, little economic injury results; whereas in Nebraska and farther south, where two or more occur, the injury to young pine is severe. It is doubtful if this insect will ever be an important pest under climatic conditions that permit the development of only one generation per year.

The life history of the insect in the East and in the West is very similar but varies somewhat more than is usually the case with the same species. The adult moths of both are small, with a wingspread of less than ½ inch. The front wings are marked with conspicuous copper-colored bands and spots. They emerge in the early spring and deposit their eggs on the tips of the young trees. After the eggs are hatched, the tiny pale-brown larvae mine the buds or needles and also the expanding growth (Fig.

82). In the latitude of Nebraska the larvae have completed their growth by the latter part of June. They then transform to the pupal stage, which they spend in a thin silken cocoon, within the tunnels that they have mined in the tips. During the first part of July they emerge as adults. These moths of the first generation then deposit eggs on the young pine tips for the production of a second generation. This second brood is much more numerous than the first and does a correspondingly greater amount of injury. When the larvae of the overwintering generation reach maturity, they spin a cocoon in which to pass the winter. The eastern variety passes the winter in the tips, while the larvae of the western variety, when full grown, drop to the ground where they spin their cocoons in the soil beneath the trees.

FIG. 82.—Adults of the Nantucket pine-moth, *Rhyacionia frustrana bushnelli*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

The history of the Nantucket pine-moth on the Nebraska National Forest illustrates well one of the dangers that foresters should guard against in conducting reforestation projects. The Nebraska Forest is made up of a series of plantations isolated from native pine. Under such conditions, it might be expected that the forest would, at least,become well established before any injurious pests would make their appearance in it, provided, of course, that reasonable precautions were taken to prevent insect introduction. But because of the desire to obtain quick results in the early days of this project, the advantage of isolation has been sacrificed. Instead of waiting the 3 or 4 years necessary to produce planting stock from seed in the local nursery, forest-pulled stock was shipped in from the Lake states and the Black Hills for planting in Nebraska. Inasmuch as this stock appeared to be healthy its introduction was deemed safe. But if we examine the available evidence, it would appear that the Nantucket pine-moth found its way into the plantations on some of these forest-pulled trees. The insect, although innocuous in the north, became an exceedingly serious pest in its new home.

The introduction of a parasite, *Campoplex frustranae*, has materially reduced the Nantucket pine-moth population in Nebraska, but it still continues to be a serious pest in pine plantations in the South. No satisfactory control for this insect has as yet been developed.

The European Pine Shootmoth.—In recent years, the European pine shootmoth has received much attention because of the serious injury that it has caused in pine plantations in certain places, notably in Connecticut. Much fear has been felt that this insect, which has now spread into most of the New England states and westward to Illinois, might invade the stands of native pine in northern New England and the Lake states. This danger now seems remote because it has been shown that the insect is unable to withstand successfully the severe winter temperatures characteristic of most of the natural northern pine areas (West, 1936). A minimum temperature of −18°F. will result in the nearly complete destruction of the shootmoth.

It is and probably will continue to be a serious pest in pine plantations in southern New England and other localities with a similar climate. It can be controlled by spraying the trees in midsummer with either lead arsenate or derris applied with a suitable spreader (Friend, 1938).

The Pales Weevil.—Another important pest of young pines, particularly in the Northeastern states, is the pales weevil, *Hylobius pales*. This weevil is normally a secondary pest of pine but, under certain conditions, it may be extremely injurious to seedlings (Peirson, 1921). It is said that one important reason for the failure of natural reproduction of white pine, following logging, is the injury to seedling growth by this beetle (Fig. 83).

The pales weevil is a small, brown snout-beetle with light-colored markings on the elytra. It breeds in freshly cut logs, stumps, and injured trees, depositing its eggs in the bark during the early spring months. The larvae develop to full growth in the cambium region and are grub-like in form, resembling the young of the bark beetles. When full grown, they form pupal cells by cutting depressions in the surface layers of the sapwood and roofing them over with shredded wood. This type of pupal cell is often called a *chip cocoon*. The adults emerge in the spring months and before they begin ovipositing they require fresh phloem of white pine for nourishment. In cutover pine

areas, the small seedlings provide almost the only green white pine available. For this reason, in the spring, the young trees are attacked and sometimes entirely destroyed by hungry adult weevils.

The planting of recently logged white-pine areas should not be attempted until after the second season following logging, unless some means are used either to destroy the brood or to prevent the breeding of this weevil in the fresh stumps. On logging

FIG. 83.—A white-pine seedling injured by adults of pales weevil. Note how the bark has been gnawed off. (*H. B. Peirson, Harvard Forest Bull.* 3.)

areas where a good advance growth of seedlings is already established when the large trees are cut, it is advisable to treat the stumps to prevent breeding of the weevil. This end may be accomplished by barking or scorching the stumps. Barking can be done for only a few cents a stump for those averaging 14 inches in diameter and is much cheaper, and more effective, than scorching stumps with fire.

The White-pine Weevil.—One of the important meristem insects of the eastern white pine in the sapling stage is the white-pine weevil, *Pissodes strobi*. This pest does not kill trees, but, by killing the terminal shoot of the main stem, it causes the trees

to grow forked and crooked and may, under some conditions, render them unmerchantable for lumber (Graham, 1926, MacAloney, 1932).

The weevils are brown snout-beetles somewhat smaller than the pales weevil and with more sharply distinct white markings on the elytra. They pass the winter in the litter beneath the trees. In the spring, they emerge from hibernation to feed for

FIG. 84.—A white-pine weevil adult, resting on the terminal buds of a white-pine sapling. Feeding punctures may be seen on the buds, and oviposition punctures on the stem below the buds.

a time upon the buds and inner bark of the leading shoots of young white pines. They then deposit their eggs in chambers hollowed out of the inner bark (Fig. 84). From one to three eggs are deposited in each chamber. The grub-like larvae work downward beneath the bark and destroy the phloem as they proceed (Fig. 85). Full growth may be attained before the first whorl of branches is reached, but in some instances the larvae may pass below the second, or even the third, whorl from the top before reaching full development. When full grown, the larva, after constructing a pupal cell in the pith or wood, transforms to the pupa and then to the adult (Fig. 86). In late July and August the young adults emerge; after feeding for a short time

upon the inner bark of the new growth, they seek hibernation quarters beneath the trees.

Although this insect is primarily a pest of sapling pines, its activities are not confined entirely to such trees. Sometimes large trees may be attacked, but the injury that results is negligible. The age at which the trees are most susceptible is between

FIG. 85.

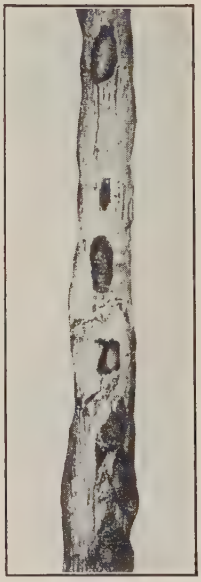


FIG. 86.

FIG. 85.—Section of a white-pine terminal shoot with the bark removed to expose the eggs and larvae of the white-pine weevil.

FIG. 86.—Larvae and pupae of the white-pine weevil in their pupal cells within the pith of a white-pine shoot.

10 and 15 years. After the 20-year mark is passed the proportion of infested leaders falls rapidly and soon becomes of little consequence.

This pest can be controlled in ornamental plantings by pruning from the trees the injured shoots, or by collecting the adults during the early spring, by knocking them off the trees into a large

net. Either collecting or pruning is too expensive to be profitably applied to forest plantations for the purpose of reducing the weevil population alone; but when this practice serves the double purpose of destroying the weevil and at the same time preventing the injury from extending below the topmost node, it may be profitable (Cline, 1933).

Studies in New England, New York, and Minnesota have all shown conclusively that trees growing in a dense stand are less subject to weeviling than are trees growing in open stands and, also, that in dense stands the stimulation to straight growth is so

FIG. 87.—A scattered stand of young white pine where stimulation to straight growth is lacking. Such pines are certain to be heavily injured by the weevil and will seldom produce merchantable timber.

strong that practically all weevil injury is outgrown (Fig. 87). For perfect results 1,700 trees per acre is necessary in New York, whereas the standard density of 1,200 trees per acre gives adequate protection under Minnesota conditions.

It has also been shown by Peirson (1922) and others (Graham, 1918) that white pines growing under the shade of hardwoods are not attacked by the white-pine weevil. This suggests the possibility of growing white pine under a nurse crop, or under a modification of the shelterwood system, so as to maintain such conditions of light as to be unfavorable for the weevils but still suitable for satisfactory growth of the pines. The planting of white pines in mixture with other pines has also been suggested

as a possible means of reducing injury by the weevil. In selecting trees for such mixed plantings it should be remembered that other trees such as norway spruce, jack pine, and some other species are also susceptible to the attack of this weevil.

Many white-pine plantings have been unduly weeviled because of open spacing or other reasons. Unless this damage can be repaired, they will not produce any valuable wood. Cline and MacAloney (1931) have shown that good results may be obtained by pruning the proper number of final crop trees so that they will recover from weevil injury, and at the same time liberating these trees from competition where necessary to insure their success in the stand. They show that, by an average expenditure of $18 per acre, badly weeviled plantations will yield at least a twenty-fold return when the crop is cut in from 25 to 40 years.

Other Tip Insects.—Numerous other meristem insects attack the terminal parts of trees and some of them are decidedly injurious, although most of them are usually not important as pests. Several species of Pissodes, such as *Pissodes terminalis*, on lodgepole pine, *Pissodes engelmannii*, on engelmann spruce, and *Pissodes sitchensis*, on sitka spruce, are very injurious. Numerous small bark-beetles belonging to such genera as Pityophthorus, Scolytus, Pityogenes, Orthotomicus, or Ips, and buprestid or cerambycid borers like Agrilus, Callidium, and Neoclytus are frequently observed working in the phloem of the terminal parts, but most of these are secondary and need not be considered at length here. References to some of the more important species will be found in the bibliography.

INSECTS FEEDING ON SMALL ROOTS

All the meristem insects that have been considered so far in this discussion, which feed on the terminal portions of trees, have attacked the parts above ground. A group that feeds upon the small rootlets beneath the ground will now be discussed. Members of this group are, for the most part, enemies of small trees only, because the roots of the larger trees penetrate the ground below the depth at which these insects normally feed, and are consequently little affected by them. Both trees growing in nurseries and seedlings in the forest, however, often suffer severely as a result of the activities of root-eating insects.

The White Grubs.—The most important meristem insects feeding on rootlets belong to the white-grub group represented by the species of the genus Phyllophaga (Lachnosterna) and other related genera. The genus Phyllophaga is by far the most important, however. These insects are closely related to the very injurious European genus Melolontha. The phyllophagous white grubs are the larvae of the may beetles, the large, awkward beetles of the family Scarabaeidae (Fig. 88). The beetles are

Fig. 88.—White grubs. Adult and larvae. (*University of Minnesota.*)

about ½ inch or more in length, heavy-bodied, and brown or black in color. They emerge from the ground in early spring and feed upon the foliage of trees. Occasionally, they cause considerable defoliation injury. At times woodlands, especially oak woods, may be completely stripped when the beetles are abundant.

The females deposit their eggs in locations close to the adult food plants. Proximity to adult food seems more important than the kind of vegetation covering the ground (Yeager, 1938). They also find favorable locations for their eggs in the nursery in coniferous seedbeds. The numerous species vary somewhat in their life cycles, but in general it is as follows: The young feed

for the remainder of the summer upon organic material and roots near the surface of the soil. When winter comes, most species[1] burrow deep into the ground and hibernate. The next spring they work their way upward toward the surface and continue to feed on the roots of trees or herbaceous vegetation. With the arrival of fall, they again burrow deeply into the ground for hibernation, and again in the spring they continue to feed upon roots. The larval growth is completed in midsummer, after which the larvae make pupal cells in the ground where they transform to the pupal stage. After an interval of a few weeks, transformation to the adult takes place, but the beetles remain in the ground until the following spring. Thus 3 full years is usually required to complete the life cycle. In the south, the cycle may be reduced to 2 years, but in the extreme northern part of the United States and in a large part of Canada, completion of the cycle requires 4 years or possibly 5 years. Those species that have a 3-year life cycle are most injurious during the second season, when the large larvae feed actively throughout the summer. During the first season the larvae are too small to cause much damage and in the third summer only a brief period is spent in eating and the greater period in the prepupal and pupal stages. Those having a 4-year cycle are especially injurious during the second and third seasons.

These insects are sometimes exceedingly injurious in forest nurseries, particularly in transplant beds. There is still much to be learned about white grubs, both in forest nurseries and in plantations. It appears that, in nurseries, serious injury almost always occurs in locations that are within a few hundred yards of the food plants of the adults. Oak is one of the favorite adult foods for several of the more important species. Others feed on aspen, paper birch, juneberry, New Jersey tea, and many other woody plants, including pine in a few instances.

The beetles feed at night and pass the day in the soil where they lay their eggs. Formerly, it was thought that the beetles would oviposit only in soil that was covered by vegetation, but this is not correct, as their oviposition has been observed in nursery paths and bare areas of washed sand. Thus the older recommendation to screen the beetles out of seedbeds might not

[1] One important species in the Northern forest areas, *Phyllophaga drakii*, remains near the surface during the winter.

prove effective unless the entire nursery were screened. The cost of this would, in most instances, be prohibitive.

The best advice that can be given at present is tentative. It would seem advisable to determine the food plants of the Phyllophaga common in the locality of the nursery and remove these trees or shrubs from the vicinity of the nursery for a distance of 300 or 400 yards.

Treating the soil with lead arsenate, as recommended for the Japanese beetle (Fleming, 1937) is dangerous in forest nurseries because in the sandy, acid soils on which most of these nurseries are located there is serious danger of arsenic injury to the young trees. On heavier soils containing a higher proportion of organic and colloidal material, it is safer.

In the Roth Nursery in Michigan, where the proximity of oak results in a continuous infestation, the grubs are controlled by mechanical means. The beds are examined frequently for injury, and the grubs are located and removed from the soil with a stiff, pointed wire like a knitting needle. This method is, of course, expensive.

In forest plantations, the damage from white grubs is sometimes tremendous. In the Lake Superior State Forest and the Marquette National Forest in Michigan the grubs have completely destroyed many plantations. In other places, periodic injury occurs. It is not at all uncommon, however, for grubs to destroy from 10 to 25 per cent of the planted trees in a single season. At present, little can be done to prevent such loss except to avoid planting on lands heavily infested with grubs, pending the time when research now in progress may indicate how this may be done safely.

Various species belonging to genera of lamellicorn beetles other than Phyllophaga also feed on the roots of trees but are not nearly so dangerous (Yeager, 1937). Some of these genera are Serica, Diplotaxis, Macrodactylus, Dichelonyx, Pachestethus, and Anomala. Some of these may be more important as defoliators than as root eaters. For instance, *Pachestethus oblivia* is becoming an important defoliator of jack pine, and *Macrodactylus subspinosus* frequently defoliates oak.

Root Weevils.—Several root weevils belonging to the genus Brachyrhinus, particularly *Brachyrhinus ovatus*, the strawberry root-weevil, are sometimes very injurious to coniferous trees in

the nursery (Gambrell, 1938; McDaniel, 1932). This insect is a general feeder that attacks many different kinds of plants. The larvae live in the soil and eat bark from the small roots. This stripping of the roots results in the death of the trees. The adults feed upon the foliage and bark. Almost all species of conifers are attacked, but the beetles in a locality may have a special preference for certain species. Hemlock, white cedar, and various spruces are attractive food for them.

The adults are small, black weevils, about ¼ inch long, with the head pronged only slightly into a broad snout. They cannot fly, which probably explains to some extent the spotty character of their infestations. The larvae are typical legless weevils and lie in a curved position in the soil when at rest.

These insects have one generation per year. The young adults emerge from the pupal stage late in June, and after a period of feeding, begin to oviposit. A certain proportion of the adults may live over winter. Gambrell's observations indicate that this is about 20 per cent. Presumably they continue to oviposit throughout the growing season, but the greater proportion of eggs is deposited during June and July. There is, however, considerable variation from year to year.

Soil treatments with arsenicals have not proved effective in destroying the larvae. Gambrell and McDaniel both recommend the use of poisoned baits containing an arsenical or 5 per cent of sodium fluosilicate. This should be applied in the evening, sprinkling it on the ground. The first application should be made as soon as the beetles appear in large numbers in the spring. This treatment should be followed by two more applications during June.

Gambrell found that some control could be obtained by spraying, with calcium arsenate, the trees on which the beetles were feeding using 6 pounds per 100 gallons, with a suitable spreader, presumably calcium caseinate. It was not so effective as the bait, except in wet weather.

Other Small-root Insects.—In addition to the white grubs and weevils there are a number of insects of lesser importance that feed upon the small roots of trees. Some of the cecidomyid gall insects attack the root meristem and there produce galls. Some other members of the Diptera also may attack the small roots but they are all of minor importance from the economic view-

point. Some of the soil-inhabiting insects, like the wireworms, will feed upon the small roots and, if numerous, may cause considerable injury to seedlings either in the forest or the nursery.

The wireworms belong to the family Elateridae of the order Coleoptera and, like the white grubs, feed in the larval stage upon vegetable material, including plant roots. The adults of this family are commonly called *click beetles*. They are heavily chitinized, flattened beetles resembling some of the buprestids in form. The larvae are slender, elongate, and heavily chitinized; hence the name *wireworm*. The legs are feebly developed.

These insects are found most commonly in comparatively heavy, moist soil which contains a considerable amount of undecayed plant materials. Small trees growing in such locations are most likely to suffer injury from these pests. No satisfactory method has been developed for the control of wireworms; forest nurseries, therefore, should not be established on soil in which wireworms are abundant.

CHAPTER XII

MERISTEM INSECTS OF THE PHLOEM REGION

The insects of this group are commonly known as *phloem insects*. They live in the phloem and the adjacent cambium and soft tissues of the xylem throughout their developmental period. With certain groups, the Scolytidae for example, even the adult life is spent for the most part in that region. Among the phloem insects are some of our most destructive forest pests and, also, many species that never kill or seriously injure healthy trees. Representatives of several insect orders live in the phloem, but most of them belong to either the Lepidoptera or the Coleoptera. For purposes of discussion, it is more convenient to divide the phloem insects into two arbitrary groups, namely, the phloem borers and the bark beetles. Insects belonging to both these groups feed upon the inner bark during the developmental stage, but in the former group only the larvae, and in some cases the pupae, are found in that region, whereas in the latter group both larvae and adults inhabit the phloem.

PHLOEM BORERS

Among the phloem borers are members of both the Lepidoptera and the Coleoptera, the latter predominating. Among the Lepidoptera the pitch moths are perhaps the most common (Fig. 89). There are a number of species of these moths, but their life cycles and types of injury are usually very similar. Therefore the well-known pine pitch-mass borer adequately illustrates these lepidopterous phloem insects.

The Pine Pitch-mass Borer.—The adult of the pine pitch-mass borer, *Parharmonia pini*, is one of the clear-winged moths of the family Aegeriidae. In shape and coloring, these moths suggest wasps; consequently, members of this family are frequently cited to illustrate protective coloration and mimicry. This insect does not kill trees but causes defects that lower the value of lumber made from the injured trees.

The adult moths appear in midsummer and deposit their eggs on the bark of the host tree, usually at the edge of a wound. The larvae, which are typical caterpillars in form, hatch from the eggs and spend 2 or 3 years in the developmental stages. During this period they feed in the phloem and adjacent tissues, where each larva excavates a broad chamber near the point where the

FIG. 89.—A pitch pocket in the process of formation in douglas fir. The growth of the tree is gradually enclosing a mass of pitch exuded from the tunnels of the douglas-fir pitch-moth. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

egg was deposited. After the larvae have become full grown, which process may require several years, they transform to the pupal stage in the pitch mass that has accumulated over the burrow. Just before the adult moth is ready to emerge, the pupa works the anterior portion of its body out of the sticky mass of resin, so that the moth may emerge without becoming entangled in the soft mass.

The control of pitch moths is very difficult in the forest. The systematic examination of the trees, in order to secure the destruc-

tion of larvae by mechanical means, has been recommended for certain species, but such an operation would be economically justifiable only where extremely severe infestations occur in very valuable timber. Because the moths seek wounds and scars for oviposition, the prevention of mechanical injuries to the tree, or any treatments that tend to stimulate rapid healing of wounds, will reduce the amount of injury by the pitch moth. Thrifty trees growing on suitable site conditions are less susceptible than are trees growing on the poorer sites. On shade and ornamental trees, of course, the process of destroying the larvae is both effective and economically justifiable.

By far the greater number of the important phloem borers belongs to the order Coleoptera. Among them are many of the Buprestidae, the metallic wood borers or flat-headed borers; and a number of Cerambycidae, the long-horned or round-headed borers. These families of beetles contain some of our best known forest pests. Some of them are primary and are able to attack healthy trees and complete their development therein. Others are secondary and are able to complete their development only in decadent or dying trees, and in freshly cut logs. The secondary species play an important part in hastening the death of overmature and decadent trees (Hall, 1933) and in hastening the decay of forest waste by opening the way through the bark for fungous infection, but otherwise they are of little direct importance. This is not true of the secondary insects discussed in the next chapter, those that not only work in the cambium region but also bore into the solid wood.

A few examples of the phloem beetles will now be considered. Several of the primary species that are representative of the important families mentioned above will be discussed.

The Sugar-maple Borer.—Among the phloem borers one of the most striking and best-known examples is an insect of the family Cerambycidae called the *sugar-maple borer, Glycobius* (*Plagionotus*) *speciosus*. This insect confines almost all its larval activities to the phloem and adjacent tissues. Only when it reaches its full growth does it penetrate into the sapwood, where it forms its pupal cell.

The adults are beautiful black beetles, almost 1 inch in length, with yellow markings (Fig. 90). They emerge from the trees in midsummer and deposit their eggs in slits, which they cut with

their mandibles in the bark of sugar-maple trees, usually on the trunk. The larvae soon hatch, tunnel through the bark, and take up their injurious labors in the phloem region. Here the larvae pass the winter and in the year following they accomplish the greatest injury. Since the larvae tend to tunnel around the tree rather than lengthwise of the trunk, a very few of them working close together, may girdle a tree and thus kill it. Usually, however, the larvae are not gregarious and consequently the infested tree does not immediately die. The killing of patches of bark opens the way, however, to the attack of other disease organisms. The larvae attain full growth by the end of the summer following the year of oviposition. At that time they tunnel into the wood where the pupal cell is formed; there the second winter is passed in the prepupal stage. The pupal stage occurs the following summer just previous to the emergence of the adults. Thus a period of 2 years is required for the complete life cycle of this insect.

FIG. 90.—The sugar-maple borer, *Glycobius* (*Plagionotus*) *speciosus:* 1. Adult beetle. 2. Young larva. 3. Fully grown larva cutting into the wood. (*Felt, "Manual of Tree and Shrub Insects."*)

To control this insect in shade trees, it is advisable to destroy badly infested trees. In moderately infested ornamental trees, the larvae may be cut out and destroyed. This work should be done as early as possible in the life of the insects so that the resultant wounds may be small and, as a result, quick to heal. The presence of young larvae is indicated by the exudation of frass and sap from the egg slits. In woodlands and groves, the presence of a luxuriant undergrowth is said to reduce the danger of infestation by this beetle. The beetle is a light-loving species; hence trees in the open are more subject to attack than are trees

in closed stands. This fact should be borne in mind when improvement cuttings and thinnings in hardwood forests are contemplated.

The Two-lined Chestnut-borer.—The two-lined chestnut-borer, *Agrilus bilineatus*, is a member of the family Buprestidae. The members of this family are sometimes called the *metallic wood borers*, because of the metallic coloration that is so characteristic of the adults; or sometimes they are called *flat-headed borers*, because of the flattened prothorax, which at first glance appears to be the head of the larva. Many of the members of this family are phloem-wood insects and some are wood insects. These will be taken up in succeeding chapters. But some of them, like the two-lined chestnut-borer, work during their entire developmental period in the phloem region.

The two-lined chestnut-borer attacks chestnut, oaks, and, possibly, beech. It is generally distributed east of the Rocky Mountains. The beetles after emerging in late spring and early summer deposit their eggs upon the bark of their host trees. They are black beetles about ½ inch in length and rather slender in form. These beetles are more or less gregarious, and the eggs that the females lay are usually deposited rather close together on attractive portions of the trunks and larger branches of the host tree. Like the eggs of most other buprestids, these are tightly fastened to the bark, and, in hatching, the young larvae cut their way through the underside and bore directly through the bark to the phloem. There they tunnel transversely between the bark and wood. Working in groups as they do, they promptly girdle the infested portion of the trunk or branch and may, if they are sufficiently numerous, kill a large tree in a single season (Fig. 91). The larvae are elongate flattened grubs with the head invaginated into the somewhat enlarged flat prothorax. By autumn the larvae are full grown. They tunnel into the bark and there form pupal cells in which they pass the winter as prepupae. In the spring they transform to the pupal stage and in June emerge as adults.

The two-lined chestnut-borer is a light-loving insect. The adult beetles like to bask in the sun. Hence they are much more likely to deposit eggs upon trees that are standing alone than they are upon forest trees. This species is, therefore, more injurious to shade trees than to trees growing under forest conditions. In

some localities, the two-lined chestnut-borer is frequently found working along with the root rot, *Armelaria mellia*, a parasitic fungus. Armelaria, unlike the borer, appears to attack most frequently trees growing in woodlands and kills groups of trees. Around the edges of these killings, the two-lined chestnut-borer finds a desirable place and usually joins with the fungus in continuing the destruction of the trees. A tree that is heavily

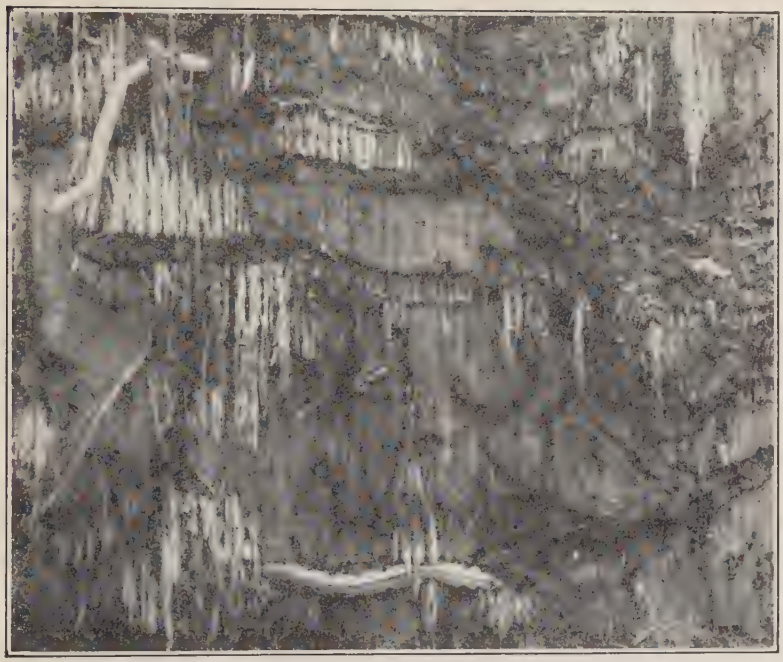


FIG. 91.—Larvae of the two-lined chestnut-borer, *Agrilus bilineatus*, tunneling in oak. (*University of Minnesota.*)

infested by this insect is almost certain to die; the tunnels resulting from a light attack, on the other hand, are often overgrown by healthy vigorous trees.

There is a difference of opinion concerning the primary character of this beetle. Some believe that it attacks only decadent trees and that it is not a serious pest in healthy oak stands. This may be true, but available evidence indicates that, in the Northern sections of the United States, oaks of the black-oak group that are apparently growing under normal conditions are frequently killed by this insect. Farther south, however, conditions

are more favorable for the growth of oak. There, only decadent trees seem to be attacked.

Evidence is accumulating to indicate that such a situation is not unusual and that trees growing in the most favorable part of their range are much less susceptible to insect injury than those growing near the outer limits, where conditions are less desirable.

Furthermore, shade trees are very often grown under conditions that are distinctly unfavorable, and therefore are more subject to injury than trees growing under natural forest conditions. For this reason, it is necessary to use special care to maintain the health of such trees, and, in the forest, to maintain a normal stocking and natural conditions. Grazing and burning of oak woodlands endanger the health of the forest and may lead to the attack of such insects as the two-lined chestnut-borer.

One of the methods frequently suggested for the control of the two-lined chestnut-borer is to cut and bark all infested trees and burn the bark before the adult beetles emerge in the spring. Control by this method must be a community project if it is to be a success. The efforts of an individual owner, without the support and cooperation of his neighbors, are hopeless. Even when an entire community joins in the work, there is danger of the beetles flying in from outside and reinfesting the area.

Almost the only way to control the two-lined chestnut-borer on a small scale is by the use of a repellent spray. Whitewash, lime sulphur, and iron sulphate have a repellent effect when applied to the trunk and large branches, in that they make the tree less attractive to the beetles. Unfortunately, most repellent materials lose their efficacy as a result of the effects of rain; hence, in order to insure success, frequent applications of the repellent must be made during the period of oviposition.

Other Species of Agrilus.—Several other species of the genus Agrilus are dangerous enemies of forest and shade trees. The oak twig-girdlers are particularly injurious. These girdlers attack small branches or twigs and usually carry their tunnels toward the base of the branch in which they are working. At intervals they circle the branch and thus girdle it at that point. These insects may kill branches as large as 2 inches in diameter; thus they stand in an intermediate position between the meristem insects of the trunk and larger branches and those that work on twigs.

In many parts of the United States, the bronze birch-borer, *Agrilus anxius*, has made almost impossible the growing of birches for ornamental purposes. Even in the forest, overmature stands, slow-growing birches on poor sites, and trees left on cutover areas are attacked and killed by this insect (Fig. 92).

FIG. 92.—Work of the bronze birch-borer, *Agrilus anxius*, in white birch. (*University of Minnesota.*)

Like the two-lined chestnut-borer, it stands on the border line between the primary and secondary insects. It appears, however, that many trees, especially those on cutover lands, that have apparently been killed by this borer, have actually been suffering from adverse physical effects that would have destroyed the tree even without the borer (Hall, 1933). In other instances, subnormal trees that might survive for years may be attacked and killed.

Therefore, the control of this insect depends to a considerable extent upon the care that the trees receive. Proper mulching, fertilization, and irrigation of shade trees may protect them for years against the attack of this beetle. In the forest, it is dangerous to log in such a manner that birches in the residual stand are left in an exposed position. If exposure of such trees cannot be avoided, they should, in the interest of economy, and to prevent the excessive multiplication of the borer, be removed and utilized at the time of logging.

In order to leave the mixed hardwood forest in a safe condition, from the entomological viewpoint, the group selection system seems to be more desirable than a system that calls for the selection of individual trees. By group selection, it is possible to avoid unduly exposing especially sensitive trees like the birches to adverse physical conditions. Pure stands of paper birch cannot be handled on any selection system without undue danger from exposure and insects.

Melanophila Beetles.—Several buprestid species of the genus Melanophila have attracted considerable attention. One of these is the hemlock borer, *Melanophila fulvoguttata.* This insect is a flattened, metallic, black beetle with three small white spots on each elytra. The larvae are slender legless grubs with the widened prothorax characteristic of most buprestids.

Since 1932, much mature hemlock in the Lake states has died. These trees have almost invariably been heavily infested with the hemlock borer, and superficial examination suggests that it was the cause of death. Ordinarily, this species is supposed to be secondary, limiting its attacks to decadent trees and felled logs. Examination of the tree rings of hemlock indicates that the trees in northern Wisconsin and Michigan that survived the 1922 outbreak of the hemlock looper had recovered prior to 1930. Beginning in 1932, there occurred a period of excessively slow growth due apparently to drought conditions. The year 1935 was the only normal year until 1937. The year 1938 was wet. During the period from 1932 to 1938, the mortality of hemlock was excessive. It seems possible that drought was the primary, and the hemlock borer the secondary, cause of this.

On cutover lands, the residual hemlock reacts very much as does the birch. When left in exposed positions, it usually dies as the result of exposure or by a combination of exposure and borers.

Hemlock is very sensitive to trampling about the roots and soon is attacked by insects and succumbs under such treatment. Therefore, it is inadvisable to depend on this tree for shade on camp and picnic grounds. Ordinarily, hemlock groves should not be used for such purposes.

FIG. 93.—Adults of *Melanophila californica*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

The eggs of the hemlock borer are deposited in groups deep in the bark crevices, where they are firmly cemented. The young larvae penetrate directly through the bark to the inner phloem. If conditions are unfavorable for them, they do not reach the cambium, but cut transverse tunnels in the inner phloem until they soon die without seriously injuring the tree. If conditions are favorable, they penetrate the cambium and construct tortuous frass-filled galleries just outside the wood until their

FIG. 94.—Larvae of *Melanophila californica*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

growth is complete. Then they cut their pupal cells in the outer bark and pass the winter as prepupae. The following spring they emerge during June and July, mate and oviposit, thus completing the life cycle.

Another species, *Melanophila californica*, is an important insect in overmature ponderosa-pine forests of California and Oregon, especially on the drier sites (Figs. 93, 94). This species attacks apparently healthy trees, especially in the top. Often the attack may be unsuccessful for a number of years, and the larvae will be able to make only very small galleries before they are killed.

FIG. 95.—Larva of *Melanophila californica*. Showing healed-over scar of the early mine, and larva extending mine later when the tree is about to succumb. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

These galleries are quickly overgrown by wood. Only when the tree is at the point of death are the larvae able to develop to maturity.

It is thought that repeated unsuccessful or incipient attacks by this beetle may so weaken the trees that they become subject to the attack of the western pine-beetle. Whether or not this is true remains to be proved, but it seems evident that the presence of incipient flat-headed injury is an indication of a subnormal condition that is conducive to dendroctonus attack (Fig. 95).

BARK BEETLES

We now come to the second arbitrary group of phloem insects, the bark beetles of the family Scolytidae (Ipidae). They comprise a very large family of the Coleoptera. A large proportion of both the genera and species of this family is represented in North America. Each larger group of the family has a characteristic manner of working, and there is much variation in the details of the life cycle of different species even within a genus. Almost all the members of this family are tree-inhabiting insects.

General Characteristics.—Certain traits and habits are common to all the bark beetles. For instance, all the true bark beetles excavate galleries in the phloem and there deposit their eggs. The larvae that hatch from these eggs work outward in the succulent tissues of the inner bark and cambium until they are full grown. There they form pupal cells, sometimes in the outer sapwood, sometimes between the bark and wood, and sometimes in the outer bark. The pattern formed by the tunnels is specific in character (Figs. 96, 97). An expert can usually easily identify a species of bark beetle by its work alone.

Most of the bark beetles are secondary in character, but a few species are important primary pests. Some appear to stand in the middle ground and are usually secondary, although they may occasionally become primary. Only under conditions favorable for them are these intermediate forms able to attack and kill living trees. The balsam-fir bark-beetle, *Pityokteines sparsus*, is an example of a bark beetle that appears never to be primary. *Ips pini*, *Ips perroti*, and *Pityogenes hopkinsi* are usually secondary, but, when they occur in excessively large numbers, they may occasionally kill a few young trees. Other species of Ips, particularly some of the western species such as *Ips emarginatus* and *Ips oregoni* may become primary temporarily and attack living trees, especially in the upper parts (Figs. 98, 99).

The Pine Bark-beetle.—Although the bark beetles of the genus Ips are, as a rule, secondary in character, they are so common that questions concerning them and their activities are continually arising. For this reason a representative of this genus has been selected for consideration here. The pine bark-beetle, *Ips pini*, is an extremely common species throughout the eastern half of the United States and Canada, and may at times become primary.

Its habits and life history are very similar to that of other species of the genus. The adults of this bark beetle are small, black beetles about $\frac{1}{8}$ inch in length. As is the case with all the members of the genus, the caudal portion of the elytra, called the *declevity*, is concave and bordered on each side with spines.

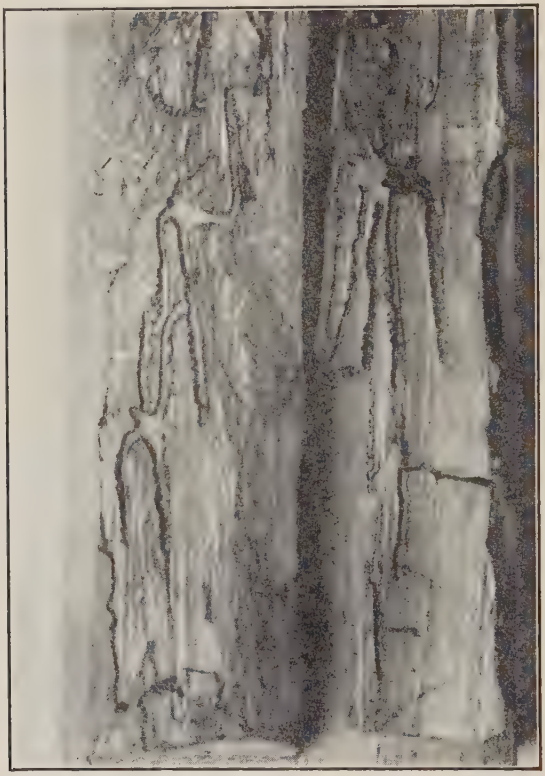


FIG. 96.—Tunnels of *Ips calligraphus* in white-pine bark. This type of gallery, with the central nuptial chamber and radiating galleries, is characteristic of many of the Scolytidae.

In the opinion of Trägårdh (1930) this modification is useful for keeping the galleries free of frass and represents a very high degree of specialization. The declevity gives the beetle the appearance of having the rear end of the body cut off sharply. The beetles attack freshly cut or unhealthy pines and, to a lesser extent, spruce. The male excavates a chamber in the inner bark, termed the *nuptial chamber*. Radiating out from this central chamber

are cut several egg galleries, each occupied by one female. The females, in cutting their egg galleries, push the frass back into the nuptial chamber, and the male relays it to the outside. When the nuptial chamber becomes clogged, the females stop work until it is cleared; or, in case of the death of the male, they cease work entirely. As the egg galleries are extended, eggs are deposited along the sides in niches. These hatch, and the larvae work out in the cambium at right angles to the egg gallery. When development is completed, a pupal cell is formed at the end of each larval mine. Here the pupal stage is passed.

FIG. 97.—Galleries of the pine bark-beetle, *Ips pini*.

The young adults feed for a short time in the inner bark and then emerge to seek fresh material in which to establish a new generation. In the North there is but one generation of this species during a single season, but in the South there may be as many as three, and possibly more, because of the longer and warmer season. Most bark beetles pass the winter in the bark of their host trees but the pine bark-beetle hibernates in the litter on the ground (Fig. 100).

Control of the pine bark-beetle, and of other species of the genus, is usually unnecessary, but occasionally, under some circumstances, they may be sufficiently injurious to require protective measures. For instance, during the recent years of excessive drought in the Southeastern states, much timber has been killed by these beetles. In other instances, where

logging is carried on periodically and not continuously, beetles of this genus, and other bark beetles that normally breed in slash, may become temporarily primary and may kill some living timber, particularly seedlings and saplings.

FIG. 98.—Tunnels of *Ips oregoni*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

Because of the danger that secondary insects breeding in slash may become temporarily primary, it is always desirable to carry on logging operations at an approximately uniform rate, so that the beetles from the slash on one cutting area may be absorbed in the fresh slash on the adjacent area. If this system is followed, there is little danger that slash insects will be an important factor in most forests. Where intermittent or scattered operations are necessary, however, a certain amount of loss must be expected,

unless the slash is cared for in such a way as to reduce the abundance of slash insects. The usual methods of burning slash do not accomplish this end, because only the small portions of the waste material are burned. The larger pieces, like broken or culled logs and stumps, offer the best places for the breeding of

FIG. 99.—Galleries of *Ips emarginatus*, the three-branched gallery, and *Dendroctonus monticolae*, unbranched gallery, in the phloem of ponderosa pine. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

potentially injurious species of insects. Therefore, it is these parts that should be cared for, either by barking them or by piling over them the finer slash.

The pine bark-beetle is one of the insects that often causes the loosening of bark on rustic buildings. Rustic material may be protected from this kind of injury either by careful sun curing, or by treating the bark with some repellent, like creosote

or carbolineum, before it is used for either buildings or furniture.

References to other species of secondary barkbeetles will be found in the bibliography.

Dendroctonus Beetles.—Of all the bark beetles, those belonging to the genus Dendroctonus are by far the most important primary enemies of living trees. The tremendous annual losses occasioned by the attack of these beetles have already been discussed. All the species of this genus are not equally injurious,

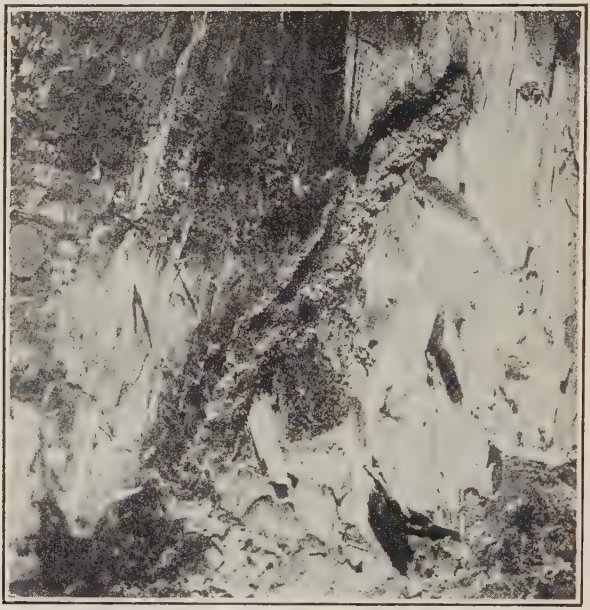


FIG. 100.—A gallery of the red turpentine-beetle, *Dendroctonus valens*. Note the egg nitches cut along the side of the gallery.

however. Some, like *Dendroctunus valens*, the red turpentine-beetle, and *Dendroctonus terebrans*, the black turpentine-beetle, are almost always secondary. Most species are pests of mature timber under ordinary circumstances, but when they become epidemic some, like the Black Hills beetle, attack indiscriminately any tree, above 6 inches in diameter, regardless of size or condition.

The most important species of this genus are: the Southern pine-beetle, *Dendroctonus frontalis;* the spruce-destroying beetle, *Dendroctonus piceoperda;* the Black Hills beetle, *Dendroctonus*

ponderosae; the mountain pine-beetle, *Dendroctonus monticolae;* and the western pine-beetle, *Dendroctonus brevecomis.* At times other species like the douglas-fir bark-beetle, *Dendroctonus pseudotsugae* and *Dendroctonus valens* (Fig. 100), may become abnormally abundant.

Each species of Dendroctonus differs in its habits, so that it is not easy to generalize concerning either their biology or their economic status. Even the same species may behave differently in various parts of its range so as to require variations in methods of treatment. On the other hand they all have features in common.

One important characteristic common to all the important economic species is their gregarious habit of attack. They select certain trees or groups of trees and attack in force. This manner of attack results in the prompt death of the tree and a minimum flow of resin to hamper the activities of the beetles. Although the beetles are able to cope with a moderate amount of resin for a short time, they would be overwhelmed or driven from the trees by a continuous or copious flow. For this reason even the most aggressive species are not able to attack successfully as individuals. Even when a moderately large number of beetles attack a particularly vigorous tree the attack may not succeed. Such a failure is indicated by the presence of numerous large pitch tubes on the bark.

The life history of the different dendroctonus beetles differs in detail but is similar in many respects. The adult beetles cut egg galleries in the inner bark along the sides of which the eggs are laid. The larvae work out from the egg tunnels, feeding on the phloem. When full grown they form cells in either the phloem or the outer bark where they pupate, transform to adults, and later emerge. The winter is passed in all stages except the pupa. In the spring the adults construct new galleries for brood rearing; the old larvae pupate, transform to adults, and likewise start new attacks; while the young larvae continue development in the tree where they overwintered. As a result, adults are emerging throughout the season, but the height of emergence is in midsummer. In the North and at higher elevations there is usually one generation, or one and a partial second generation, but in warmer localities there may be several generations during a season.

CHARACTERISTICS OF DENDROCTONUS BEETLES

Common name	Specific name	Size and color of adults	Egg galleries	Larval mines	Pupal cells	Number of generations	Common host trees
Western pine-beetle	*brevicomis*	3 to 5 mm. Dark brown to black	Winding between bark and wood	In phloem little exposed on inner surface	In outer bark	1 and partial second to 2 and partial third	Ponderosa pine Coulter pine Lodgepole pine (rarely)
Southern pine-beetle	*frontalis*	2.2 to 4 mm. Brown to black	Winding between bark and wood	Practically all in phloem	Outer bark except thin-barked trees	3 to 5	Shortleaf pine Loblolly pine and other pines and spruce in S.E.
Mountain pine-beetle	*monticolae*	3.7 to 6.4 mm. Brown to black Head with frontal groove	Elongate Usually straight but sometimes sinuous	Grouped alternately on opposite sides of egg gallery. Exposed on inner surface	In phloem Usually exposed on removal of bark	1 and a partial second	Lodgepole pine Sugar pine Western white-pine Ponderosa pine White-barked pine
Black Hills beetle	*ponderosae*	3.7 to 6.4 mm. Brown to black Resembles *monticolae*	Similar to *monticolae*	Similar to *monticolae*	Similar to *monticolae*	1 and a partial second in northern part of range	Ponderosa pine Lodgepole pine Limber pine Engelman spruce Mexican white-pine
Douglas-fir beetle	*pseudotsugae*	4 to 7 mm. Red to dark brown Hairy	Vertical, sinuous or straight Usually 12 to 14 in. long. Occasionally 30 in. or very short	Fan-shaped groups Mostly in phloem but may engrave wood. On alternate sides of egg gallery	In phloem May or may not be exposed when bark is removed	1 and a partial second	Douglas fir Western larch Bigcone pine (Usually secondary)
Eastern spruce-beetle	*piceaperda*	4.5 to 6.2 mm. Reddish brown to black	Vertical straight 6 to 8 in. long	Grouped on opposite sides of egg gallery. First in phloem, later between bark and wood	Between bark and wood. Engraving wood	1 generation	Mature Black spruce Red spruce White spruce
Engleman spruce-beetle	*engelmanni*	5 to 7 mm.	Short, straight, slightly engraving wood	Similar to *piceaperda*	Between bark and wood	1 generation	Mature Englemann spruce
Red turpentine-beetle	*valens*	5.7 to 9.5 mm.	Irregular winding or straight gallery at base of tree	Grouped along egg gallery and work in mass formation	Between bark and wood	2 or more	All pines and occasionally spruce, larch, and fir. (Primary on Monterey pine, otherwise secondary)

The egg galleries vary in form and serve as diagnostic characters. The southern pine-beetle and the western pine-beetle both cut winding galleries between the bark and wood, and the pupal cells are constructed in the outer bark (Fig. 101). The mountain pine-beetle and the Black Hills beetle both construct elongate, longitudinal egg galleries and pupate in the phloem.

The control of dendroctonus beetles has been the subject of

FIG. 101.—Tunnels of *Dendroctonus brevicomis* in ponderosa-pine bark showing degrees of attack. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

research for many years, but the methods in current use today are essentially those used by Hopkins in 1906. They consist of the direct destruction of brood on the assumption that the resultant population reduction will save green trees that otherwise would be killed.

The details of the method are varied depending upon the size of the timber and the habits of the beetle to be controlled. In general the procedure may be divided into the following steps:

1. Scouting to determine the location and extent of the infestations.
2. Marking infested trees for treatment.
3. Cutting, barking, or burning the trees and destroying the brood (Fig. 102).

Scouting may be of an extensive nature and conducted by looking over a timbered area from points where views may be obtained, that is, from high elevations, from lookout stations, or from airplanes. Or it may be conducted in various degrees of intensity by means of strip surveys.

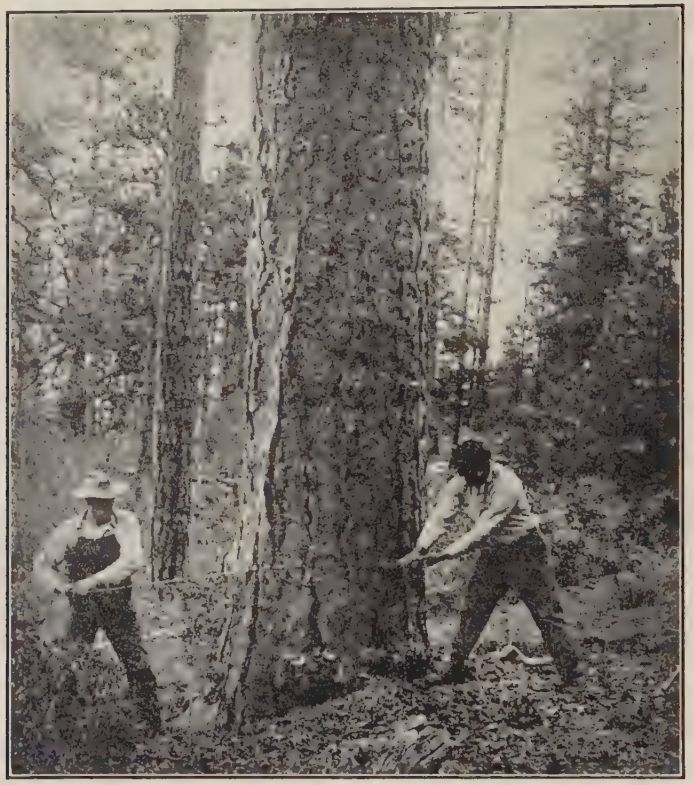


FIG. 102.—Felling a western yellow-pine infested by *Dendroctonus brevicomis*. (*F. P. Keen.*)

After the infested areas have been located the marking of the infested trees is done by men trained to recognize the presence of beetles in the trees. In the case of early-season attacks it is possible to recognize the infested trees by the change in crown color, but later attacks may produce no foliage change before cold weather sets in. In such instances the only evidence of the beetles' presence will be the exudation of frass and pitch from the entrance holes.

The color phases through which the trees pass after attack are first a slight paling of the needles followed by fading to a greenish yellow and finally to red. Red tops are of course the most conspicuous, but trees showing this characteristic no longer indicate a bark-beetle hazard, because the brood will have emerged from the tree by the time the foliage has reached the red stage. The pale and greenish-yellow tops are those that indicate the presence of the beetles in the trees. The red tops are, of course, not

FIG. 103.—Barking a tree infested with *Dendroctonus brevicomis*. The first step in destroying the broods. (*F. P. Keen.*)

marked for cutting, but are an aid in indicating where to look for newly infested trees.

An attempt is made to mark every infested tree in a control area, and, in order to do this, the markers must examine every tree for signs of fading, for active entrance holes, or for both. In order that no trees will be missed, the area is examined in contiguous strips, each marker examining and marking for treatment the trees in his own strip. The width of the strips may vary with conditions, but a common width is two chains. Two to four spotters work together under the direction of a compassman, who runs an accurate compass line and records the size and location of marked trees and other pertinent information.

The control operations are usually conducted in the fall or spring but may be carried on at any convenient season except

during the heavy flight of the beetle, when it will be impossible to find the infested trees effectively. Weather conditions permitting, winter is an excellent time for control work. The method of treating the trees varies with their size and the habits of the species of beetle present. Small trees are usually cut into convenient lengths, decked, and burned, unless they can be promptly utilized. Large trees, after felling, are barked on the top and sides and, in the case of beetles which pupate in the outer bark, like the western pine-beetle, the bark is piled in a row close

FIG. 104.—Burning the bark removed from a tree infested with *Dendroctonus brevicomis*. This final step is necessary in order to kill the insects in the pupal cells within the bark. (*F. P. Keen.*)

to the sides of the log and burned (Figs. 103, 104). If the fire hazard is high, as it often may be in the summer, so that burning is dangerous, the bark may be laid out in the sun, which will raise its temperature above the point fatal for the beetles. Small logs may be treated by solar heat (Patterson, 1930) by first exposing one side until the beetles have been killed, and then rolling them over to expose the brood on the underside to the effect of the sun's heat.

Other methods of destroying the brood have been used, and still others are now under experimentation, but none of these have come into general use. One method that has been used to some extent in the Rocky Mountain region is the method of burn-

ing standing. This consists of spraying fuel or gas oil onto the infested boles, igniting it, and, as the flames spread to the top of the sprayed portion, throwing more oil at that point in order to force the fire to crown. This method should result in the destruction of 90 per cent of the brood, but it is applicable only in stands where the fire hazard is not too high. It has been most used in lodgepole-pine stands. Burning or scorching the felled trees by using oil may sometimes be advantageous. For burning standing a nonexplosive type of fuel oil with a flash point of 160°F. and a specific gravity of 32° to 34°Bé. and for trees on the ground ordinary fuel oil with a flash point of 225°F. and a specific gravity of 27°F. have proved most suitable (Keen, 1938).

Experiments in injecting poisons into the infested trees to kill the brood have been partially successful, and spraying the bark with a lethal oil also holds possibilities of success, but no method has as yet been developed to replace cutting followed by burning or barking.

The evaluation of results in bark-beetle control projects is difficult. In some instances, they seem to have been successful, whereas in other instances, little benefit has been derived. An analysis of results (Craighead, 1931) of control projects over a period of 30 years indicates under what conditions control operations are usually desirable for the western species. A few of the more outstanding conclusions are presented here for the three most important species.

In all instances, control should be undertaken only on the basis of a careful survey to determine the extent of the infestation, the degree of isolation of the infested area, and the trend of the outbreak, whether increasing or decreasing. Control is never profitable except on an infestation that is on the increase. Under endemic conditions, when the beetles confine their attack to injured and decadent trees, control does not pay. In all control operations, it seems essential that every effort be made to locate and treat all infested trees on a control area. Furthermore, it is obvious that, in accessible areas, control should be combined with utilization of the materials cut.

Dendroctonus brevicomis is one of the most serious pests of mature ponderosa pine from California to Montana. In the mixed forest on the west slopes of the Sierra Nevadas and the Cascade Mountains, it seldom becomes epidemic, and then only

for two or three seasons. Control there is usually not justified, except to protect stumpage values on small areas. On the dry east-side types, control is justified on areas where utilization is possible, on isolated small areas, on at least partially isolated large areas that can be completely covered in a single season, and in park and recreational areas where the aesthetic values justify larger expenditures than do the timber forests. In the northern Rocky Mountains, this species is not usually serious, but in case of outbreaks, the broken character of the ponderosa-pine stands is advantageous for successful control.

Dendroctonus monticolae is a most serious enemy of lodgepole and western white-pine in the northern Rocky Mountain Region and of sugar pine in southern Oregon and California. It also attacks ponderosa pine but is usually not serious on that species. Neither is it usually serious on the high-elevation type of lodgepole in the Sierra Nevadas, although there have been some severe outbreaks in this type, especially following defoliation epidemics.

In the northern Rocky Mountain Region, prompt detection and control of small increasing infestations are justified, in order to prevent this aggressive species from getting out of hand. This is especially true in the lodgepole type, where outbreaks of this beetle have spread for hundreds of miles through continuous lodgepole forests. Where regular logging operations can be conducted in infested areas, arrangements should be made to leave fresh logs on the ground during the flight period, to attract the emerging beetles and thus protect standing trees. Later, when the logs have become infested, they will be utilized and the broods destroyed. In western white-pine stands, their relatively broken and isolated character justifies local control of rising infestations.

Control of outbreaks of this species on high-elevation lodgepole in the Sierras is usually not economically justifiable, except in parks and recreational areas. In such places, it is recommended, if aesthetic values are such as to justify the expense involved and if all infestations over several thousand acres can be treated. In sugar pine, control can usually be accomplished in a single season and is desirable in the case of increasing infestations.

Dendroctonus ponderosae is similar in appearance and habits to the mountain pine-beetle. It attacks ponderosa pine in

the Black Hills, the central Rocky Mountain Region, and the Colorado Plateau. Because it is an aggressive species like the mountain pine-beetle, it is advisable to keep a close watch of conditions and immediately suppress all rising infestations. Green logs for traps should be left on the ground during the flight period of the beetles. Later utilization will destroy the brood. With the possible exception of sugar-pine infestations it is usually impossible to bring dendroctonus beetles under control in a single operation. Therefore it is essential to repeat each year for

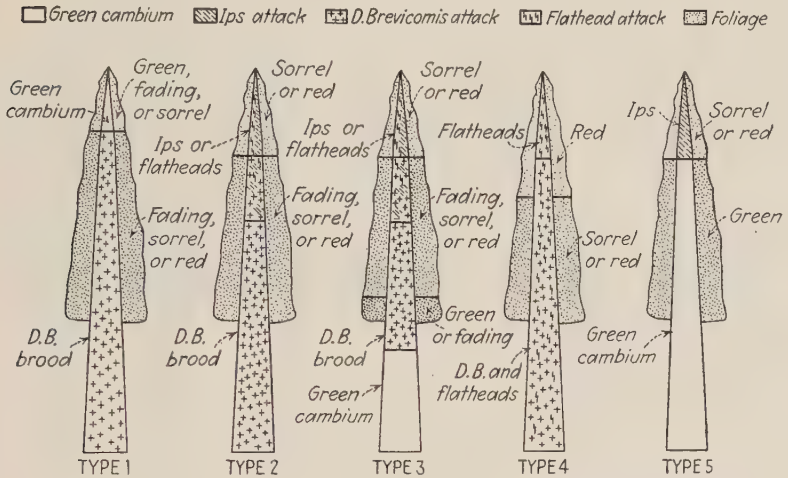


FIG. 105.—Population composition of insects in ponderosa pine based on studies in California. Color phases indicate the order of attack by various insects. From this figure it will be seen that trees apparently killed by *Dendroctonus brevicomis* may have been attacked previously by other insects. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

several years control operations in order to reduce the beetle population to a safe level. Sometimes, when weather conditions are especially favorable for the beetles, practically continuous control may be necessary if disastrous outbreaks are to be prevented.

There are many things still to be learned about dendroctonus beetles, but it seems evident, however, that they are, on the whole, enemies of mature or overmature timber. Except in epidemic periods they prefer decadent and injured trees. Ecologically, they seem to be one of nature's means of harvesting overmature timber. It seems likely that they may ultimately cease

to be especially important after the existing timber reserves have been utilized or brought under management. Then they will probably be held in check by the regular operations involved in managing timber stands. In the Black Hills region, this state already seems to have been reached.

At present, in many localities in the West, the fate of the existing forest depends upon the entomologist and his ability to cope with the dendroctonus problem. Good forest practice on a sound and permanent economic basis requires that continuous

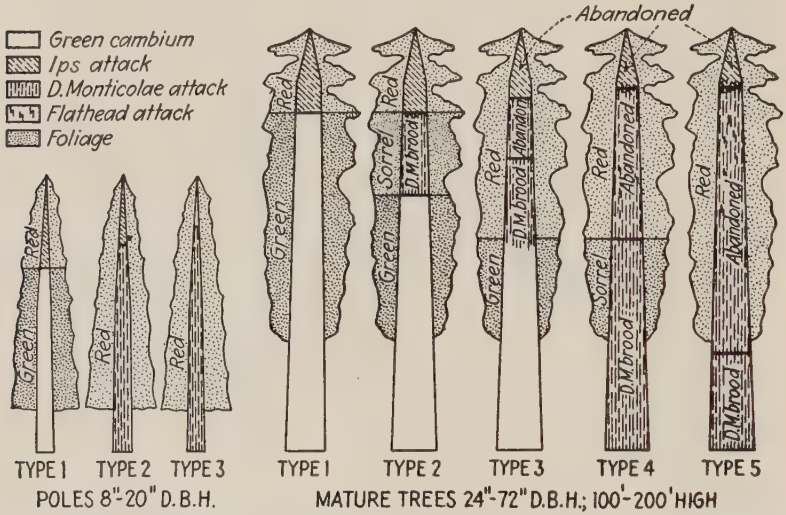


FIG. 106.—Population composition of insects in sugar pine. Color phases indicate successive attack from top to base of the trees, sometimes starting with an Ips attack. Thus observations limited to the basal portion of the trunk of a dying tree may not indicate true conditions. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

production be maintained. This can be accomplished only when the forests are operated on a sustained-yield basis that provides for the use of wood at a rate no faster than it is produced. It follows from this that existing reserve stands must be removed over a long period of time if the normal distribution of age classes essential to the sustained-yield forest is to be attained in the next tree generation (Figs. 105, 106).

During the past decade, timber owners, both public and private, have seen their reserves shrink at an alarming rate, owing to beetle attack. Naturally they fear for the loss of their

investment and are therefore inclined to cut off the merchantable timber as rapidly as possible before it is killed by the beetles. Unless these owners can be assured that beetle losses can be prevented, it seems almost certain that unregulated and excessively heavy cutting of reserve stands will continue.

In order to make possible the regulation of logging that will lead toward sustained yield, Western forest entomologists have been attacking the problem from other angles than direct control.

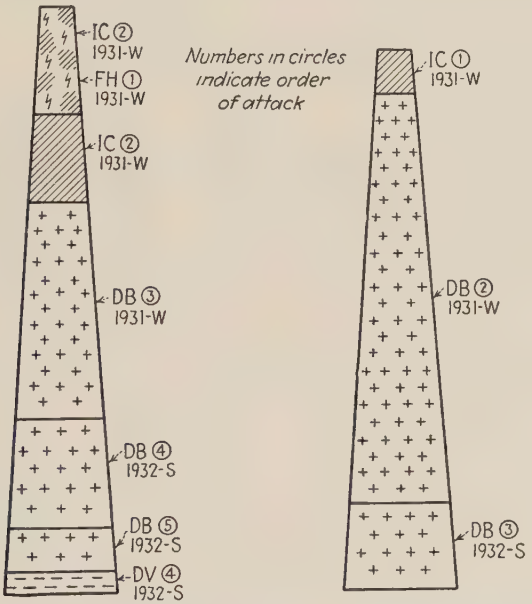


FIG. 107.—Tree diagrams of typical attack in overmature ponderosa pine on the dry, East-side type. Trees of this type are especially susceptible to beetle attack when overmature. *FH.* Melanophila. *IC. Ips calligraphus. DB. Dendroctonus brevicomis. DV. Dendroctonus valens.* (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

The character and composition of beetle infestations have been analyzed to determine the causes of attack (Fig. 107). On the basis of past beetle history of the stands, timbered areas are being classified into hazard classes, with the idea that logging operations can be concentrated in the areas of greatest risk. It seems likely, of course, that units where the risk is now low will eventually pass into the high-risk class; for the present at least, it seems safe to reserve such stands.

Other attempts have been made to classify ponderosa pine on the basis of relative individual susceptibility. Keen (1936) has proposed a classification for this species and has determined the coefficient of infestation for the various classes. This is intended to serve as a guide in marking timber that is to be cut selectively. Under this classification, the trees are divided into four age classes and four subclasses, based on crown and foliage characteristics (Fig. 108).

KEEN'S PONDEROSA PINE CLASSES AND RISK

Class 1.—Young trees less than 75 years old. Bark dark and crown pointed.

A. Full crown 55 per cent of tree height. Average width or wider. Foliage dense, long, dark green. *Risk very low.*
B. Fair crown. Less than 55 per cent of tree height and less than average width. Foliage not sparse. *Risk slight.*
C. Fair to poor crowns. Brush top narrow and thin. Foliage short and thin. *Risk very high.*
D. Crown poor. Diameter subnormal. Foliage sparse and thin. *Risk very high.*

Class 2.—Immature trees 75 to 150 years old. Bark reddish brown with narrow or incompletely formed plates. Crown pointed and branches in whorls.

A. As above. *Risk very low.*
B. As above. *Risk slight.*
C. As above. *Risk very high.*
D. As above. *Risk very high.*

Class 3.—Mature trees 150 to 300 years old. Bark light reddish brown with moderately large plates. Usually round topped. Incomplete whorls with nodes indistinct. Branches horizontal or drooping.

A. As above. *Risk low.*
B. As above. *Risk medium.*
C. As above. *Risk medium.*
D. As above. *Risk highest.*

Class 4.—Overmature trees over 300 years old. Bark light yellow. Plates large and smooth. Crown flat. Branches drooping, gnarled, and crooked.

A. As above. *Risk high.*
B. As above. *Risk high.*
C. As above. *Risk high.*
D. As above. *Risk highest.*

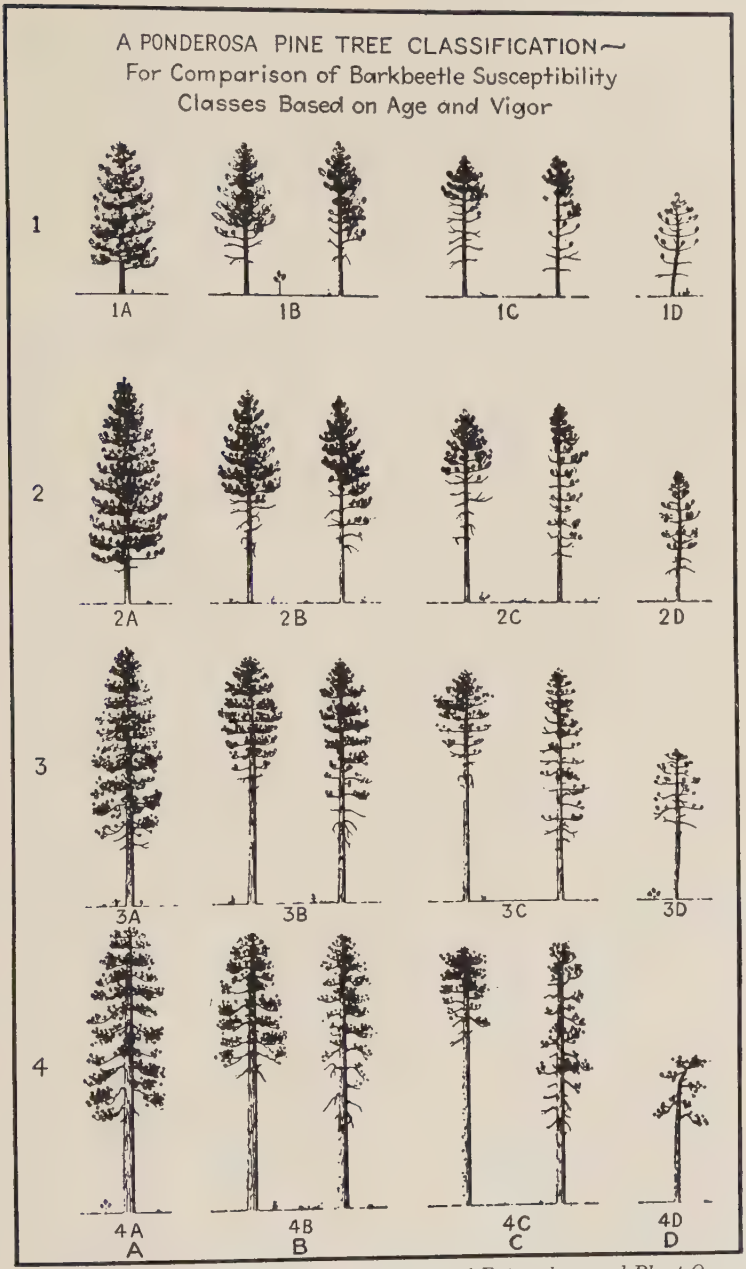


FIG. 108.—Keen's tree classification. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

Salman in California is also grouping trees according to amount of risk on the basis of crown and foliage characteristics. He divides them into four risk classes and assumes that the presence or absence of incipient flat-head attack indicates whether or not the risk is high or low. He has not as yet formally defined his classes, but in actual field-marking tests, he and his men are able to select with a reasonable degree of success the trees that show incipient flat-headed attack on the basis of crown characteristics.

The cause of most outbreaks of dendroctonus beetles is not known, but it appears that periods of dry weather are often correlated with outbreaks of the western pine-beetle and the southern pine-beetle. In the case of the mountain pine-beetle and the Black Hills beetle, it seems probable that weather is also important in favoring or discouraging multiplication. Blackman believes that the time rain occurs is more important than the amount. Rain just prior to emergence is helpful, whereas rain during the flight period is harmful. Ordinary slash does not seem to be a dangerous breeding place for dendroctonus beetles, but windfalls may produce high populations that may start outbreaks. Forest fires and defoliation may frequently be followed by dendroctonus outbreaks.

Some of these causes are in part controllable, but, if overmaturity and weather are the chief factors responsible for outbreaks of dendroctonus beetles, the possibility of preventing epidemics in overmature stands seems remote. Therefore, the most logical procedure is to harvest first the most susceptible trees, on the basis of best available information and, when outbreaks occur, apply direct control when it promises to pay a satisfactory return.

CHAPTER XIII

PHLOEM-WOOD INSECTS

The last group of meristem insects are those that attack both phloem and wood. They are commonly called *phloem-wood* insects. For the most part, these insects are pests of dying trees and freshly cut logs. In some cases, however, they attack living trees.

PESTS OF LIVING TREES

Some of the outstanding examples of phloem-wood insects that attack living trees are the locust borer, *Cyllene robiniae*, the poplar borer, *Saperda calcarata*, the carpenter worm, *Prionoxystus robiniae*, the linden borer, *Saperda vestita*, the willow borer, *Cryptorynchus lapathi*, and the leopard moth, *Zeuzera pyrina*. Space permits of a discussion of only the first three of these species. Information on other species may be secured by consulting the reading references given in the general bibliography.

All the insects of this group work in the phloem for a time after the larvae hatch and later penetrate into the wood. Their work in the meristem is usually of comparatively short duration and is generally not sufficiently extensive to result directly in the death of the trees. As a result of this, the chief injury caused by the activities of the insects of this group is a reduction in quality of lumber, or the mechanical weakening of standing trees, or a combination of weakening and reduction in grade. In addition to these direct effects, the phloem-wood insects open the way for fungous infection and thus materially hasten decay.

The Locust Borer.—One of the best-known examples of phloem-wood insects that attack living trees is the locust borer, *Cyllene robiniae*, a member of family Cerambycidae (Fig. 109). At one time the black locust in eastern United States was considered one of the best trees for posts, poles, and railroad ties because of its rapid growth and the durability of locust wood.

Many plantations of this species were set out in Pennsylvania and in the Ohio and Mississippi valleys. Today, a large proportion of these plantations have been abandoned as valueless because of the ravages of the locust borer.

In recent years there has been a great increase in the planting of black locust as a result of the activities of the Soil Conservation Service. This tree is especially desirable for producing a quick cover on eroded lands. A corresponding increase in the economic importance of the locust borer has resulted.

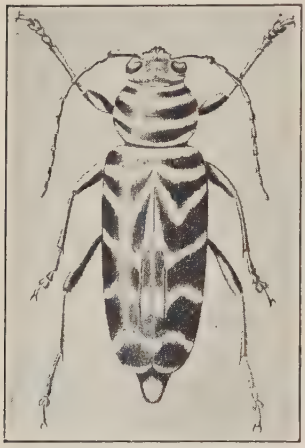


FIG. 109.—Adult of the locust borer, *Cyllene robiniae*, enlarged about one-third. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

The adults of the locust borer are beautiful black beetles, ½ to ¾ inch in length, with narrow yellow crossbands on the elytra (Fig. 109). The beetles emerge in late summer and autumn. They deposit their white eggs in clusters of five or six in cracks and crevices in the rough bark of black locust trees. Young trees under 1½ to 2 inches in diameter, and older trees over 5 to 6 inches in diameter, appear to be comparatively unsusceptible to attack, although if a tree is once infested it may remain subject to infestation regardless of size. Thickness and surface character of the bark appear ordinarily to be the factors that determine the susceptibility of the tree to attack. The bark must be sufficiently old to be rough, but must not be so thick that the young larvae cannot bore through it. This limitation of attack to certain specific age classes aids greatly in formulating plans for the control of this insect.

In a short time after they are deposited, the eggs hatch, whereupon the young larvae cut their way through the bark to the inner phloem. Here they feed until cold weather forces them into hibernation. The winter is passed in the larval tunnels. In the spring the larvae continue their work in the phloem for a short time before entering the wood. Examination of infested trees will readily disclose whether the larvae have entered the wood, or whether they are still in the phloem, because while they

are working in the phloem they cast a brown-colored frass out of openings through the bark; whereas after they enter the wood they push from their burrows a yellowish-colored frass. Throughout the life of the larvae an opening from their burrows to the outside is maintained, through which the frass is ejected. For a time, the entrance hole serves this purpose, but later, as convenience demands, other passages are cut to the outside. The larvae, after completing their growth in late July and August, excavate cells in the wood in which they transform to the pupal stage, and later, in the same season, to the adult. Thus the life cycle is completed in 1 year.

Control of the locust borer has proved to be difficult, especially on the poor sites characteristic of eroded lands, on areas strip-mined for coal, and other similar places where locust has been planted. The work of Craighead (1919) indicated that locust grown in a dense stand is free from serious attack by the borers. This he attributed to the sun-loving habits of the beetles. Recent studies by Hall and his associates in the Ohio Valley (unpublished) have shown that the oviposition response of the beetles depends more on temperature than light and that high temperatures during the oviposition period will result in heavy oviposition within the stand and cool temperatures will result in heavier oviposition on the outer trees exposed to the sun. The optimum temperature for oviposition is about 70°F.

Since oviposition occurs in late summer and fall, there is a tendency toward more heavy oviposition on the outer exposed trees. From this it appears that the maintenance of as dense a stand as possible is advantageous but cannot be depended upon to give adequate control.

Hall has shown that there is a definite correlation between rate of tree growth and the amount of borer injury. Presumably this is partly due to the shorter period during which rapidly growing trees are susceptible to attack and perhaps to an actual resistance to attack exhibited by such trees. Experiments are now under way to test promising methods of obtaining increased growth. One that appears to offer much promise is to clear-cut hopelessly infested plantations. This results in a dense growth of suckers from the roots and stumps, which grow at an almost unbelievable rate for at least the first few years.

Another promising possibility is the use of a fast-growing relatively resistant strain called *shipment locust* (Hall, 1937). This is a very desirable type that has thus far shown considerable resistance to the borer injury. It is likely that in some of the numerous plantations now being planted other resistant strains may be developed.

The locust borer is definitely favored by dry weather as evidenced by the heavy infestation and death of very large old locusts in Pennsylvania during a period of excessive drought (Craighead, 1937). Prior to this dry period these trees had not appeared to be infested.

The control of the locust borer apparently depends upon maintaining well-stocked rapidly growing stands.

The protection of shade trees is a much more expensive and difficult problem. It can be accomplished, however, in several ways. By allowing vines to climb over the trees, protection from the locust borer may be effectively accomplished. Spraying the trees with an arsenical wash of sodium arsenite in mixture with a miscible oil, or a water solution of sodium arsenate, has proved effective. In using the former mixture, 1 pound of sodium arsenite is dissolved in 20 gallons of water, to which 1 gallon of miscible oil is then added. This mixture should be sprayed on the trunks and large branches of the infested trees in the spring at the time the new growth is starting. This spray is said to kill the young larvae by penetrating into the tunnels acting as a stomach poison. Another method that is effective, though tedious, is to inject carbon bisulphide into the burrows of the insect. After injection the opening should be closed with mud, or grafting wax, to hold in the poisonous fumes. Because of labor cost, this method is suitable for use only on valuable individual trees.

The Poplar Borer.—Another important phloem-wood beetle is the poplar borer, *Saperda calcarata*. It is distributed throughout the United States and Canada wherever its host trees are found. This insect is injurious to forest trees both directly and indirectly. Directly it reduces the value of the trees it attacks by cutting large tunnels in the wood (Fig. 110). These tunnels may be so numerous in a heavily infested tree that the trunk will be much weakened, and the tree will be very easily broken off by high winds. Occasionally, when the beetles are extremely

numerous, a few trees may be killed as a result of attack by this insect but, generally, the poplar borer is not a tree killer.

This beetle does, perhaps, even more important economic damage by its indirect effects than by its direct injury. Other

FIG. 110.—Tunnels cut in solid wood by the poplar borer, *Saperda calcarata*. The curved tunnels in the upper part of the picture are pupal cells and emergence tunnels. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

injurious insects are attracted to trees that have been attacked by the poplar borer. For instance, several Buprestidae such as *Dicera prolongata* (Fig. 111) and *Poecilonota cyanipes*, often deposit their eggs in the old egg scars of the poplar borer. The carpenter worm, *Prionoxystus robiniae*, also finds that the scars

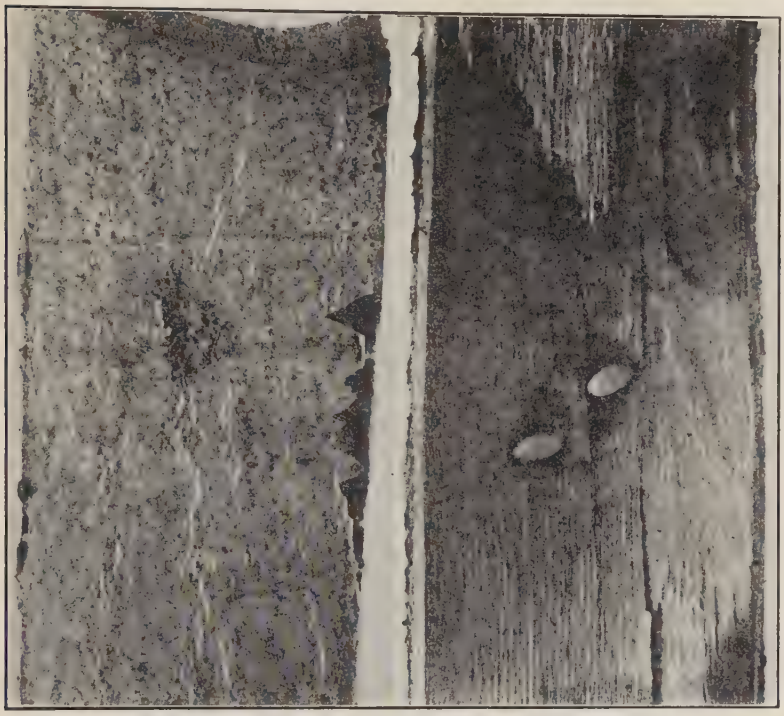
made by the poplar borer offer desirable locations for oviposition. Thus this beetle may be the indirect cause of other insect injury. Certain other habits of the poplar borer are conducive to another type of secondary injury. This insect keeps its tunnels comparatively free of frass by pushing this waste material out of openings through the bark. These open tunnels offer a ready means of access deep into the wood for the inoculum of wood-rotting fungi. *Fomes igniarius*, an important heart rot that causes a large proportion of the defects found in aspen and poplar, frequently gains entrance through these openings. In some

FIG. 111.—An adult beetle of *Dicerca prolongata*, resting on a log.

regions, it has been shown that a large proportion of heart-rot infections have arisen from insect tunnels. Thus the poplar borer and the carpenter worm are indirectly responsible for a great deal of damage that is not ordinarily charged to them.

The adult beetles are rather large, often over 1 inch in length. Their color is gray, with yellow markings. They emerge from their pupal cells in late July and August. The female beetles lay their eggs in slits that they gnaw in the bark (Fig. 112). The period of incubation is long, 20 to 25 days being required for its completion. The larvae, as soon as they hatch, tunnel through the bark into the phloem where they feed until overtaken by cold weather. The following spring they enter the wood where they spend the remainder of their developmental period tunneling through the wood (Fig. 113). In the autumn, when full grown, they hollow out a pupal cell in the sapwood. This cell is blocked off by a plug of shredded wood from the tunnel in which the insect has previously been living. The winter is passed in the prepupal stage within the pupal cell. Early the following summer the larvae transform to the pupal stage; after 25 to 30 days in that stage, they transform to the

adult, cut their way to the surface, and emerge. Thus the normal developmental period is 2 full years. In Colorado, however, at elevations ranging from 6,000 to 9,000 feet, this species requires 3



A B

FIG. 112.—The egg slit and eggs of the poplar borer. *A* shows a view of the egg slit as it appears on the surface of the bark. *B* shows the eggs in place in the inner bark. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

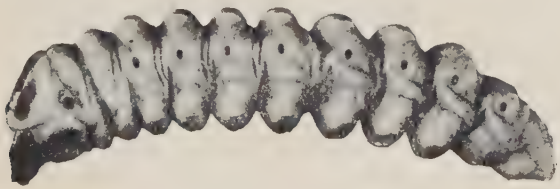


FIG. 113.—A larva of the poplar borer, *Saperda calcarata*. (*Bureau of Entomology, and Plant Quarantine, U. S. Dept. Agr.*)

full years to complete its life cycle. In warmer climates, on the other hand, it is probable that a developmental period shorter than the normal is possible.

Because of the fact that infested trees are more attractive to the poplar borer than those that are uninfested, the beetles have a tendency to concentrate upon certain trees. These favorites become very heavily infested and are sometimes called *brood trees*. By cutting and destroying these brood trees in a forest, the possible injury by this pest may be greatly reduced. After being cut, the brood trees should either be burned before the beetles emerge, or be split and ricked up in open piles in such a way that rapid drying and the heat of the sun will kill the beetles in the wood.

It has been repeatedly observed that slowly growing trees are always much more susceptible to borer injury than are rapidly growing trees. This is doubtless due to the greater ability of the fast-growing trees to overgrow wounds and scars. Such trees have a covering of smooth, healthy bark and are not so attractive as the slower-growing trees. Control measures for this insect are usually only necessary on the poorer quality sites.

The borer when working in individual trees may be controlled by painting the egg scars with carbolineum. This work should be done in the autumn after oviposition has been completed. Both the eggs and young larvae will be killed by this treatment.

The Carpenter Worm.—The carpenter worm, *Prionoxystus robiniae*, is one of the common phloem-wood insects that may well be cited as an example of the lepidopterous members of this group. It is distributed generally throughout the United States and at least the southern part of Canada. This insect was first described as a pest of black locust, hence its specific name, but it also feeds upon a variety of hardwood species. Some of the trees that are frequently attacked by this insect are the oaks, elms, and poplars.

The carpenter worm seldom kills trees. Most of its work is in the solid wood, and only in the early stages of development are the larvae phloem eaters. Although this insect does not kill trees, it is, nevertheless, a primary pest and most of its damage is done to living trees.

The adults are large gray moths with a wingspread of about 2½ inches. They emerge in early summer and deposit their eggs on the bark of a host tree. Wounds and scars on the trunk or larger branches provide the most attractive places for ovi-

position. The larvae, which hatch in a couple of weeks from these eggs, bore into the phloem where they excavate shallow galleries. After a brief period they penetrate into the sapwood and heartwood, where they spend the rest of their immature life

FIG. 114.—Larvae and work of the carpenter worm, *Prionoxystus robiniae*, in an oak tree. (*Entomological Branch, Can. Dept. Agr.*)

(Fig. 114). The larvae are typical caterpillars in form and pinkish white in color. They cut long windings galleries in the wood. These galleries are kept clear of frass so that the larvae can pass freely back and forth in them. In order to secure free passages

the borings are pushed out through holes in the bark. These holes provide an easy entrance for wood rots; consequently, these organisms are frequently associated with the work of the carpenter worm.

The length of the larval period has not been definitely determined, but in all probability it varies with differences in climate, as is the case with most other insects. In any case, however, several years are usually required for its completion. In California the life cycle requires 3 or possibly 4 years. In New York state the life cycle is said to be probably 3 years. At the end of the larval period, a pupal cell is formed in the wood near the surface and, before pupation, a hole is cut almost through the bark. The tunnel behind the pupal cell is plugged with shredded wood. The larvae then transform to the pupal stage, and, later, the moths emerge.

Almost all the investigations concerning this insect have been confined to their activities on shade trees; and as a result, although in some instances it is an important forest pest, no control under forest conditions has been developed. In shade trees, the insect can be controlled by injecting carbon bisulphide into the tunnel. Caging the trunk and larger branches of heavily infested trees to prevent reinfestation has been suggested. If the moths that emerge within the cage are killed daily, there will be no infestation from within, and the cage will effectively exclude moths from without. The cages should be kept on the trees throughout the late spring and early summer, when the moths are in flight. After the flight season is over, the cage may be removed and stored away until the next season. After a tree has been freed of infestation, caging should be continued for several years or the trunk should be wrapped with untreated building paper, until the wounds made by the borers have been completely healed. Otherwise reinfestation will be certain to occur, inasmuch as injured trees are very attractive to the moths. After the bark has completely grown over the wounds, the tree will be comparatively resistant to infestation (Burke, 1921).

PESTS OF DYING TREES AND LOGS

Representatives of those species that attack only dying trees or freshly cut logs, will now be considered. Insects of this group are important because of the loss which they cause, in both saw

logs and pulpwood, by reducing the grade of the former and the volume of the latter, not to mention the indirect injury for which they are responsible, through aiding infection by wood-rotting fungi. Craighead estimates that the loss in grade due to the activities of this class of insects amounts to about 5 per cent of the value of the annual cut. The most important of these

FIG. 115.—Adults and larvae of the flat-headed apple-tree borer, *Chrysobothris femorata*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

insects belong to the Buprestidae or the Cerambycidae of the order Coleoptera.

The Flat-headed Apple-tree Borer.—One of the many buprestids that feed on both phloem and wood is the flat-headed apple-tree borer, *Chrysobothris femorata*. This insect attacks numerous species of forest trees and also a great variety of orchard trees (Fig. 115). Some of its hosts other than fruit trees are walnut, pecan, hickory, poplar, willow, beech, oak, elm, hackberry, sycamore, mountain ash, hawthorn, redbud, maple, horse chestnut, basswood, persimmon, and box elder. Its hosts are so varied that it can almost be regarded as a general feeder on hardwoods. Because of its importance as a pest of

apple trees, this insect is called the *flat-headed apple-tree borer.* Because it is a pest of orchards as well as a forest pest, it has received more attention from entomologists than if its activities had been confined to forest trees alone. As a result, its habits are well known, and it will serve well as an illustration of the phloem-wood buprestids.

The flat-headed apple-tree borer lies in the middle ground between the primary and secondary insects. It apparently cannot attack successfully a vigorous, healthy tree but is able to attack trees that are slightly on the decline. The adult females are attracted for oviposition not only to the subnormal trees but also to healthy trees in sunny locations. They very frequently oviposit freely upon such trees. The eggs hatch and the young larvae bore into the bark, but they do not enter the phloem while the tree is in a thrifty condition. If, however, such trees should, by chance, decline in health, the larvae will promptly penetrate into the phloem and kill the tree. If, on the other hand, the tree remains in good health, the young larvae will remain in the bark for at least 1 year before they succumb to starvation. This habit has been observed in other species of the same genus, for example, *Chrysobothris dentipes,* a flat-headed borer of pine. When bark-infested trees are cut, the larvae are then able to attack the phloem and later the sapwood; thus they are able to complete their normal development in the logs.

The adults of the flat-headed apple-tree borer are short, broad, flat, beetles about ½ inch long. In color they vary from dark brown to black on the top, with grayish spots and bands, while the ventral side and the legs are bronze. They emerge from their pupal cells in early spring and are then on the wing for about 1 month. The beetles are active only on warm, sunny days. At other times they remain quiescent, hidden away beneath bark scales or in other suitable places. In warm weather they are very active, flying and running about. Experiments have shown that insects of this genus are very resistant to heat and can endure a temperature as high as 52°C. without being killed. The larvae, like the adults, are heat resistant and are able to live on the upper side of logs lying in the sun, where no other insect life can exist.

The adult beetles feed on the foliage of hardwood trees and sometimes become so numerous that they cause appreciable

defoliation. The female beetles deposit their eggs in crevices in the bark of the host trees. These eggs are pale yellow, flattened, and about $\frac{1}{20}$ inch in diameter. The young larva, after an incubation period of 15 to 20 days, bores through the underside of the egg and into the bark. So far as is known, this habit is true of all buprestids.

The thoracic region of these larvae is greatly enlarged transversely and flattened dorso-ventrally. The head is invaginated into this enlarged thorax so that only the mouth parts protrude. On casual inspection, the thorax appears to be the head of the grub, thus the name *flat-headed borer*. The larvae are helpless when removed from their burrow. Unless they have convenient surfaces against which they can expand the enlarged thorax, they are unable to move; therefore it is only in a tunnel that fits their bodies perfectly that they can move about. Thus, if a larva should cut through some portion of the egg that was not in contact with the bark, it would be helpless and unable to progress farther.

If on boring through the bark the larvae find conditions are favorable, they will construct broad feeding tunnels in the phloem and outer sapwood. They grow rapidly and in late summer are ready to bore into the solid sapwood. Here they form their pupal cells in which they pass the winter. In the South the pupal cell is sometimes formed between the bark and wood, but this condition has never been observed in the North. The winter is passed in the larval stage within the pupal cell, and pupation takes place early in the following spring.

Thrifty trees are not susceptible to this type of borer injury; this species, therefore, is only a pest of overmature, decrepit, or dying forest trees. Like many other members of this genus, it does not penetrate deeply into the heartwood and therefore is not so injurious to logs as are some other buprestids and cerambycids. It does, however, loosen the bark and make openings through which decay-causing organisms may enter, and it may tunnel to a considerable extent the outer inch of wood.

Some of the other buprestids that feed first in the phloem and later in the wood are *Calcophora virginiensis*, and *Calcophora angulicollis*. The first is an eastern species and the second a western species that attacks pines and firs. Several species of the genus Dicerca are common phloem-wood borers that may at times

cause considerable injury to the wood of dying trees and freshly cut logs.

The best way to prevent injury from these insects is prompt utilization. If this is impossible, water treatment is the next best procedure. Heavy shading of logs left in the woods will give reasonable but not perfect protection. Rustic work may be effectively treated with a refined creosote without seriously affecting its color. This will protect it against attack by phloem-wood buprestids.

The White-spotted Sawyer.—Numbers of phloem-wood insects refuse to attack standing trees until they have been severely injured or killed by some other agency. Of these the white-spotted sawyer, *Monochamus scutellatus*, is a good example. This

FIG. 116.—A white-spotted sawyer, *Monochamus scutellatus*, emerging from a white-pine log.

secondary insect is one of the most common wood-boring insects in the coniferous forests of the Northeast. It infests and reduces the value of freshly cut logs and of trees that have been severely injured or killed by fire or by other insects. This insect is so abundant, in most localities, that practically every log or newly killed tree that is left in the woods over the summer is almost certain to be infested.

The habits and life history of this species are very similar to those of other closely related species of Monochamus. The adult insects are somewhat elongate, cylindrical, black beetles about 1 inch long with very long filiform antennae (Fig. 116). The antennae of the male are twice as long as the body, whereas those of the female are only slightly longer than the body. The adult beetles emerge in spring and early summer. During the flight period they feed upon the green bark of pine twigs. Sometimes, when the beetles are abundant, numerous pine tips may be girdled and killed as a result of this feeding activity. After

feeding for a brief period, the beetles deposit their eggs in slits that they cut with their mandibles in the bark of logs and recently killed trees. Oviposition continues throughout the summer season but usually reaches its height before midsummer.

The larvae hatch from the eggs and tunnel at first in the inner phloem. They are legless, cylindrical, white grubs with powerful mandibles. They excavate broad, shallow galleries in the phloem, but as they increase in size their phloem galleries include in their depth not only the green tissues of the inner bark but also the surface of the wood (Fig. 117). Later the larvae penetrate into the sapwood and sometimes into the heartwood. When growth is completed, the larvae cut a pupal cell in the sapwood and transform to the pupal stage. The length of the developmental period varies greatly. Under favorable conditions of temperature and moisture, a single year is sufficient, but, under less favorable conditions, the life cycle may require 3 years and possibly longer. The larvae of this species, like those of the poplar borer and the carpenter worm, always keep at least a part of their tunnels clear of frass and chips. This material is cast out through openings in the bark. Like the other insects just mentioned, the pine sawyer maintains ideal conditions for the infection of the log with wood rots. These organisms are usually associated with monochamus work.

FIG. 117.—The broad, subcortical gallery of the white-spotted sawyer, *Monochamus scutellatus*. These galleries are cut during the early life of the larvae before they enter the wood.

This insect tunnels primarily in the peripheral layer of a tree or log. It is in this layer that the most valuable high-grade wood occurs. Thus, in clear logs the insect may reduce the grade of lumber sawed from infested parts from a select grade to a number 3 grade; this means a reduction in the retail value of the

best lumber from $50 to $100 per thousand feet at present prices. Furthermore, by reducing the grade of high-grade materials, the insect increases the quantity of the already too abundant lower grades, thus adding to the problem of lumber sale and distribution.

Control of the white-spotted sawyer may be accomplished in a variety of ways. Fire-killed trees should be utilized promptly or cut and kept wet with water. Prompt utilization is the best way to handle the borer problem. Water storage of freshly cut material, either by emponding or by sprinkling, is the next best solution. If neither of these methods is feasible, barking will prevent infestation by destroying the necessary green food for the young larvae. If the insects have penetrated into the wood, however, barking is useless. The cost of barking varies with conditions of labor and timber, but, in good-sized eastern white and red pine, the average cost has been approximately 10 cents per log, under ordinary conditions. Only high-grade logs should be barked. The cost of barking a low-grade, knotty log is as much or possibly more than the cost of barking a clear log, while the reduction in grade in the low-grade log is practically negligible. On the other hand the saving in grade resulting from barking a clear log attacked by the sawyer will pay many times over for the cost of barking. The one serious objection to barking saw logs has already been mentioned, namely, that the barked timber has a tendency to check badly. Suggestions have been made for avoiding this difficulty.

Where no other method of control can be used, experiments indicate that a heavy shade of brush, piled over logs left in the woods during the summer, will afford some protection from this insect. This cannot be recommended if other methods can be used, because of the inferior quality of protection afforded by this method.

This and several other species of Monochamus have at times caused considerable damage in lumber that has been freshly sawn, but not edged. The insects lay their eggs in the bark-covered edges of the boards, and the larvae work first in the phloem and then into the wood, sometimes to a depth of several inches. Still other cerambycids may cause similar injury. For instance, *Callidium antennatum* has attacked piled lumber in California. Edging the lumber when it is sawed will prevent such injury as this.

CHAPTER XIV

WOOD DESTROYERS

Although most tree insects require green meristem tissues for food during at least a part of the developmental period, certain individuals of some important groups are able to develop from egg to adult on wood alone. The insects of this group are chiefly secondary pests attacking forest products, but some of them may at times attack and injure standing green timber. Some of the wood insects require green wood, for example, the horntails; others, like the ambrosia beetles, work in either green or moist wood. The subterranean termites and the carpenter ants are not quite so exacting in their moisture requirements for they will tunnel into wood that is moderately dry. Most powder-post beetles, on the other hand, cannot work in wood unless it is thoroughly air dried.

The insects that attack and injure wood may be divided, for convenience of discussion, into several groups as follows:

1. Unseasoned-wood insects.
2. Moist-wood insects.
3. Dry-wood insects.

These are, of course, arbitrary divisions used for convenience. Under these headings various wood-destroying insects will be discussed.

The preceding paragraphs seem to imply that all wood destroyers are insects. This is not, however, the case. There are a few other groups of animals that are wood borers. The most important of these are the marine wood-borers. Because their activities are very similar to wood-destroying insects, these animals will be included in this chapter. Since they attack only moist dead wood, they will be discussed in a section following Moist-wood Insects.

UNSEASONED-WOOD INSECTS

Most unseasoned-wood insects attack the wood of dying trees or trees that have been recently killed or freshly cut. Usually

after the wood has been dead or cut for a season or more it is no longer attractive to these insects. This unattractiveness of old wood for the unseasoned-wood insects is sometimes due to changes in the moisture conditions that usually follow cutting, but even where moisture conditions apparently continue favorable, the wood after a time becomes unattractive. This is apparently due to changed physical and chemical conditions within the wood. What these changes are has never been definitely determined. There is indication that some unseasoned-wood insects may be attracted to freshly killed or cut wood by products of fermentation that disappear as the wood seasons, or as organisms of decay gain a predominant position in the wood. The fact that ambrosia beetles are not attracted to all wood even though moisture conditions are favorable, but are attracted to and attack wine casks that contain wine in storage, suggests that, perhaps, the presence of an alcohol, or of some other product associated with fermentation may determine the places chosen by the beetles for their activities. Whatever the reason for this attraction, the fact remains that the beetles are attracted only to unseasoned wood or to wood which, for some reason, simulates conditions found in unseasoned wood.

Wood Insects of Living Trees.—Although most unseasoned-wood insects attack the wood after the trees are dead or have been cut, a few find conditions to their liking in living trees. Some of these like the western cedar-borer, *Trachycheli blondeli*, are economically very important (Burke, 1928; Hopping, 1932). This insect is a beautiful metallic emerald-green buprestid that damages western cedar and cypress, especially the western red cedar. The adults lay their eggs in bark crevices on the branches of living trees, and the larvae that hatch therefrom bore long, flattened tunnels in the sap- and heartwood until they are full grown. This requires several years, during which time they leave the branches and bore extensively in the trunk of the tree. When full grown, many return to the branches to pupate. There the pupal cell is constructed within ½ inch of the surface. Transformation to the pupal stage occurs in midsummer and transformation to the adult stage about 3 weeks later. These adults remain in the pupal cell until the following season when they emerge, feed on the foliage, mate, and oviposit.

The kind of injury caused by the boring of this beetle is objectionable in poles and posts, but actually causes little, if any, reduction in usefulness of these materials. It ruins the wood for shingles, siding, shiplap, or other uses where tightness is essential. No control for the western cedar-borer in the forest has been developed. Their habits of oviposition are such as to make them very difficult to reach. The fact that certain stands are more severely injured than others suggests that ultimately silvicultural control may be possible. Burke suggests that the disposal of branches following logging might be helpful in reducing the beetle population. By using infested material for posts and poles and reserving the uninfested trees for shingles, siding, and other similar purposes the economic losses caused by this insect, might be materially reduced, although this procedure might not appeal strongly to companies in the pole business.

Another wood insect that injures standing timber is the turpentine borer, *Buprestis apricans* (Fig. 118). This insect attacks the pitchy wood exposed by fire scars and turpentining faces in Southern pine forests. It is especially injurious in turpentine operations where its activities so weaken the trunks of the trees that they become subject to wind breakage (Beal, 1932). Experments indicate that the French type of turpentine face, which is much narrower than that used in the United States, is less subject to injury by this beetle.

The golden buprestid, *Buprestis aurulenta*, in the West also attacks the pitchy wood of conifers exposed in fire scars and caused by logging machinery, lightning, and other agencies. It is quite similar in its activity to the turpentine borer in living trees, but in addition it may attack seasoned lumber (Keen, 1938) and may repeatedly infest and ultimately destroy unpainted flooring and woodwork. References to other important insects that attack the wood of living trees will be found in the bibliography.

Insects of Dying Trees and Recently Cut Wood.—Of the many insects that attack the wood of dying, recently killed, or recently cut trees (Craighead, 1930), two groups will be discussed. These are the ambrosia beetles and the horntails. Although they are grouped together here, their habits and the character of their injury are very different. Also the ambrosia beetles may attack moist wood that has been cut for some time, provided

conditions are suitable for the growth of the fungi upon which they feed. Most of their damage, however, is in unseasoned wood.

Ambrosia beetles, or pinhole borers, comprise an interesting and important group of unseasoned-wood insects. With the exception of the genus Platypus, which belongs to the family

FIG. 118.—Work of the turpentine borer, *Buprestis apricans*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

Platypodidae, these insects all belong to the family Scolytidae. Although they belong to the same family as the bark beetles, their habits are very different. Nevertheless they have many points in common. They are small, dark-colored insects, more or less cylindrical in form. They live in moist or freshly cut wood into which they cut their tunnels. The entrances of these tunnels resemble those of the bark beetles, but, because they tunnel into the wood, the frass which they cast out is light colored instead of brown. Although they bore into the wood,

they are not wood eaters; instead, they feed upon a fungus growing on their tunnel walls. This fungus is always associated with the ambrosia beetles, each group of beetles having its own specific fungus. Whenever a tree ceases to be suitable for the growth of this fungus, the beetles must leave. With them, adhering to their bodies, they unwittingly carry either the sticky spores or perhaps the mycelium. Having sought out a suitable, freshly cut tree or stump, they proceed to bore directly into the wood. For a short time they are without food, but soon the spores that they have brought with them germinate, giving rise to a new growth of ambrosia fungus.

This apparent cultivation of its food by an insect has caused many observers to ascribe a high degree of intelligence to these beetles. The facts, however, will not permit crediting too much intelligence to these interesting insects. It is nothing more than an interesting example of a symbiotic relationship between a fungus and an insect. The beetle depends upon the fungus for food, and the fungus depends upon the insect for transportation from an old host to a new one.

The arrangement of tunnels varies greatly with different species of ambrosia beetles (Fig. 119). Some like *Xyleborus xylographus* construct simple branching galleries in which the eggs, larvae, pupae, and adults are found together. Others like species of Pterocyclon excavate several secondary tunnels branching in a horizontal plane from the end of the main entrance tunnel, which is widened to form a nuptial chamber. Along these secondary galleries, chambers called *larval cradles* are excavated both above and below and parallel with the grain of the wood. Still others like species of Gnathotrychus and Trypodendron construct compound tunnels, the main gallery being cut directly into the wood in a general radial direction and the secondary galleries being cut in the same horizontal plane, but in a tangential direction. In the case of Gnathotrychus the secondary tunnels usually follow an annual ring, and the larval cradles are cut in a series above and below both the main and secondary galleries. With such species the eggs are deposited in niches, and also the larvae develop and pass through the pupal stage in them. These larvae are fed by the adult beetles, who insert plugs of the ambrosia fungus into the cradle entrances. In the species where no cradles are formed by the adult, or where pupal cells similar

in appearance to the cradles are formed by the active larvae just previous to pupation (*Platypus wilsoni*), the larvae shift for

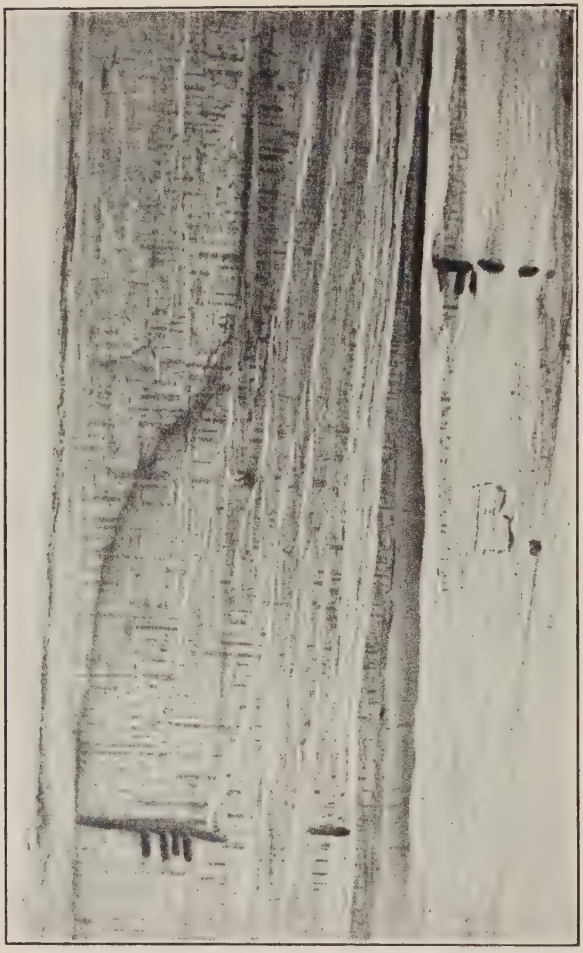


FIG. 119.—The galleries of an ambrosia beetle showing the walls stained black by the growth of fungus.

themselves, feeding upon the ambrosia fungi growing on the tunnel walls.

The ambrosia-beetle colonies are constantly faced with two problems. The first is the selection of trees in which conditions are suitable for the growth of the fungus upon which they feed. The other is to protect themselves against the growth of the

fungus itself. In the event that conditions for the growth of the fungus are not right, the larvae will starve and the adults will be forced to seek other trees. If conditions are favorable for the fungus, but the beetles do not multiply rapidly enough to consume their food as fast as it grows, the rank growth of the fungus may block the tunnels, thus smothering the beetles in their food.

There are numerous species of ambrosia beetles, most of them belonging to one of the following genera: (1) Platypus, (2) Anisandrus, (3) Xyleborus, (4) Gnathotrycus, (5) Pterocyclon, (6) Trypodendron, (7) Xyloterinus. Some of them are confined to a single species of tree, whereas others may be found in a number of species. It is probable that, inasmuch as the beetles do not eat the wood but simply use it as a place to construct their nests, the specificity of the beetles for certain trees is the direct result of the specific requirements of their particular fungus.

The injury to logs and recently killed trees by ambrosia beetles results in a decided loss in quality of the lumber and other products cut therefrom. This type of injury is serious in lumber because of the resultant reduction in grade, but it is of even greater consequence in other classes of material, for example, stave bolts and wood intended for wagon stock, or other special uses. With such materials, pinhole injury may render the product valueless.

In certain cases, however, ambrosia-beetle tunnels cannot be considered as serious defects. In oak flooring, for instance, present-day style demands a few knots and a few wormholes. These defects are said to lend character to a floor, and in some high-class homes this onetime low-grade flooring is now being used. In fact, in some instances where a grade of flooring free of these defects is furnished, small holes are actually burned in the wood to imitate the tunnels of the ambrosia beetles. In most cases, however, beetle tunnels constitute a defect that decidedly reduces the value of any forest product so injured.

Some of the greatest losses occasioned by these insects occur in the South. An unusually good example of this is found in the cypress forests. It is customary to girdle these trees some time previous to felling, so that they may dry out sufficiently to be floated out of the swamps in which they grow. Between the time of girdling and felling, the trees are often attacked and

rendered almost useless by these beetles. Other Southern tree species are often severely injured before the logs can be manufactured. Throughout the South, where the growing season is long and the number of broods is great, the ambrosia beetles

FIG. 120.—Injury to hickory caused by one of the ambrosia beetles, or pinhole borers, *Xyleborus xylographus*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

present an exceedingly serious problem. They have spelled ruin to more than one logging venture (Fig. 120).

In the North, on the other hand, several factors tend to reduce the economic importance of these insects. The long winters make possible easy logging while the beetles are dormant; this eliminates most of the injury in the woods. Furthermore, the custom of river driving the logs prevents later attack, inasmuch as logs floating in water, and frequently turned over so that all

sides are wet, are too moist to permit the growth of the ambrosia fungus.

The control of the ambrosia beetles is very difficult and entails in many instances considerable expense. They can, however, be held in check in several ways. The prompt sawing of logs followed by kiln drying provides the best and most certain protective measure, but, unfortunately, the application of this method is frequently out of the question. In general, it may be said that rapid seasoning is an important aid in the control of these beetles. This may be accomplished in large-diameter stock by barking and piling the logs or bolts in open piles. It should be borne in mind, however, that barking tends to increase checking. Wood of small diameter may be dried sufficiently by piling in loose piles without barking.

Where storage space and expense will permit, sun curing is an effective means of controlling these and other wood borers. It has previously been shown that the subcortical temperature, on the upper side of logs exposed to full sunlight, often exceeds the air temperature by 30°C. or more, and frequently passes above the point fatal to insects. By applying this principle, Craighead has shown that if logs are placed in the bright sun and are turned every week or two, the insects attacking these logs will be destroyed before they have injured the wood. In controlling ambrosia beetles, however, the logs should be turned somewhat more frequently than this. By placing the logs on long, sloping skids, they may be turned with a minimum of effort.

In cases where girdling is necessary before trees can be felled, the girdling should be done in late fall, after the beetle flight is over, in order to reduce to the minimum the injury by ambrosia beetles. It has also been suggested that inferior trees may be used as trap trees for these insects, by girdling or felling them in early spring, when the beetles are in flight. According to this plan, the beetles will be attracted to these logs or girdled trees and may be destroyed by placing the logs or trees in water, or by burning them.

One of the best and most effective methods of preventing attack by ambrosia beetles is by the water treatment. As with other insects, this may be accomplished in either of the two ways already discussed, namely, by sprinkling or by floating in water. By increasing the water content in either of these ways

the beetles are effectively excluded. Logs floating in water may be attacked on the upper side unless the logs are frequently worked and rolled over. The water treatment does not, however, give permanent immunity.

Ambrosia-beetle injury is not always confined to freshly cut or killed trees. Sometimes ambrosia beetles will attack green lumber, particularly large-dimension stock, which dries slowly. The danger of this may be greatly reduced by careful piling, so as to provide good circulation of air through and around the piles, thus encouraging rapid drying. Absolute protection may be obtained by running susceptible materials through a dry kiln.

The horntails, another important group of unseasoned-wood borers, belong to the family Siricidae of the order Hymenoptera. Like the ambrosia beetles, these are borers and attack injured trees or recently cut logs. They are very common insects and are responsible for greater damage to forest products than is usually ascribed to them. Although many species are known to science, little detailed information concerning their life histories and habits is available. They will, therefore, be treated more briefly here than might otherwise be expected. Unlike the ambrosia beetle, the horntails are for the most part true wood-eating insects (xylophagous). They work in the solid wood, maintain no opening to the outside, and are apparently not necessarily associated with any fungi. One of the largest and best known members of this group is said to be an exception to the preceding rule in that it bores only into decaying wood. This is the species known as the pigeon tremex, *Tremex columba*.

The horntail adults may be described as thick-waisted wasp-like insects. They vary greatly in size; some of them are less than ½ inch in length, whereas some are 2 inches. Black is the predominant color of the family, but nearly all species are characterized by markings of yellow or orange. At the end of the abdomen the female bears a horn-like projection from which the group name is derived.

The adults of most species fly in spring and early summer. The females, by means of their long ovipositors, attached well forward on the ventral side of the abdomen, insert their eggs into the solid wood. This is no mean feat when the flexibility of the ovipositor and the solidity of the wood into which the ovipositor is inserted are considered. Sometimes a female may

get her ovipositor wedged into the wood so that she is unable to extricate herself. Such occurrences, however, are not so frequent as might be expected. The horntails are particularly abundant and especially injurious in fire-killed forests. The scorched trees appear to be particularly attractive to the adults. Trees killed by spring fires are much more susceptible to injury by these insects than are trees killed at other seasons of the year.

The horntail larvae are white legless grubs (Fig. 121). They tunnel through the wood, cutting burrows just large enough for their bodies. The wood passes through their digestive tracts and is packed behind them as they advance. The length of the larval stage appears to be variable, even with the same species, and depends, apparently, upon conditions of temperature and moisture. With most species the larval stage is completed in one or two seasons. When growth is completed, the larvae cut pupal chambers in the peripheral layer of the sapwood. In logs the pupal cells are usually constructed on the upper side so that, although the larval work may be distributed throughout the log, the majority of the exit holes are usually on top.

Water treatment is the best way to prevent injury by these insects. In fact, it is about the only effective method to save logs except for the obvious one of prompt utilization. These borers may continue to work in green lumber sawed from infested logs. Kiln drying gives good control in sawed materials. The same results may be accomplished by raising the temperature of the wood above the point fatal to the insects, by dipping it in hot water.

MOIST-WOOD INSECTS

The insects that injure moist wood form another group of important pests of forest products. They attack wood that has been cut or dead for 1 year but is still at least partially moist as a result of contact with the ground or other moist material. Insects that work in moist wood are usually associated with protozoa, fungi, or bacteria. These organisms help the insects by converting the comparatively indigestible cellulose or the lignin into materials that are more easily digested by the insects. Because of the microorganisms present in it, moist deadwood provides more suitable food conditions for its insect inhabitants than the green wood of the freshly cut or newly killed tree. An

indirect proof of this is found in the fact that moist deadwood is attacked directly by many insects, whereas very few species can

FIG. 121.—Horntail larvae from a douglas-fir log. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

gain a living in the green wood, without either depending upon the cambium to carry them through the early stages of larval development, as the phloem-wood insects do, or by depending

for their food upon symbiotic fungi, as do the ambrosia beetles. The dietetic relationships of these organisms offer a fertile and almost virgin field for future investigations. Some of the moist-wood insects may also be found in scars in the sapwood and in the heartwood of living trees but will be included in this section because the economic losses occasioned by them are greater in forest products. Some of the wood borers, like the carpenter ants, do not obtain their food within the wood, but use their tunnels in the log or tree only for a sheltered base from which to conduct foraging expeditions and for a nursery for their young.

Insects Nesting in Deadwood.—The carpenter bees, the leaf-cutter bees, and carpenter ants are the most common examples of insects that make their nests in wood but obtain their food from outside the nest. None of them are very exacting in moisture requirements, but are most often found in wood that is not thoroughly dry. Their chief requirement, however, seems to be softness. For this reason they are often associated with decaying wood.

The leaf-cutter bees, although common, are not usually economically important, because they work singly. The carpenter bees, on the other hand, commonly work in groups, and by their combined activity seriously injure the wood attacked. Their nests are often found in wooden pillars and rails. They may be controlled by injecting an oil such as kerosene, spray oil, or orthodichlorobenzene into the tunnels.

The carpenter ants, the commonest species of which is *Camponotus pennsylvanicus*, are widely distributed in the United States and Canada. They are large black ants, sometimes ½ inch or more in length, which build their nests in soft or decaying wood, and there rear their young well protected from the attack of enemies. They are social insects, living together in large colonies. These ants do not have so many castes as do the termites, which will be discussed later, nor are they so obviously polymorphic in character, but there is a distinct division of labor within the nests. Three castes are recognized: the kings and the queens, which are the true males and females, and the workers, which are sexually undeveloped females. Although the workers are all alike in appearance, each has her own work to do. Like the honeybee, some of the workers care for the young, others care for the queen, while still others collect food. Like many other

ants, the carpenter ant may attend aphids and by husbanding noxious species may be indirectly responsible for damage by these pests.

The life history of the carpenter ant is very interesting. In brief, it is as follows: In early summer the young males and females leave the nest. Being winged at that time, they fly out in all directions. Sometimes the air may be filled with these flying ants that have emerged simultaneously from many nests. This is known as the *swarming period*, but unlike the bees, in swarming, the young males and females leave the nest at the same time, unattended by workers. It would be much better to call this the *mating flight*, for that is really what it is.

Shortly after mating, the males die while the young females may either be taken into old established colonies to replace a decrepit queen, or each may establish a new colony. In the latter case, the young queen seeks out a small cavity in a tree or piece of timber and there makes up her brood cell by completely enclosing the cavity, leaving no exit or entrance. She then breaks off her wings, for they are no longer of any use to her. After sealing herself in, she does not feed again until her first brood of young is mature (Wheeler, 1910). After depositing a few eggs in the brood cell, she hatches larvae, which are fed upon a material secreted from her mouth. The young then complete their larval development, spin their cocoons, pupate, and emerge as adults, without any other food than that furnished by the mother from her own body. The ants of the first brood are workers of very small size. As soon as they are mature they take over the work of the nest. They cut approximately parallel, concentric galleries running longitudinally through the wood to accommodate the enlarging colony and bring the organic food, on which they live, into the nest through openings cut to the outside, sometimes called *windows*. The young workers feed the queen and care for the eggs that she lays and the larvae that hatch from these eggs. They feed the young, after the first brood, upon secretions from their mouths. The nurses carry both the larvae and pupae from place to place in the nest, in an effort to keep them under the most favorable conditions; also, when the young adults are fully developed, they are assisted from the cocoon and treated with the greatest consideration. As the colony grows, more galleries are cut in order to enlarge the nest.

Carpenter ants may build their nests in a great variety of places. They may attack the dead heartwood of living trees, or they may hollow out logs, house timbers, or almost any wood materials. It has been stated, frequently, that these insects attack only decaying wood. This is not entirely true, although the original attack is usually in a decayed spot. In trees having hard wood, the work is confined to decayed wood but in trees having soft wood, like cedar, the nests are often constructed in

FIG. 122.—A nest of the carpenter ant, *Camponotus pennsylvanicus*, in a white-cedar log.

solid wood (Fig. 122). The only requirements are that the wood be soft and moist.

The carpenter ant does its greatest injury in house timbers, poles, and in standing trees with soft wood. In northern white cedar, *Thuja occidentalis*, the injury by these insects is very common; in fact, it is one of the most frequent defects of cedar. In some locations, at least 20 per cent of the trees that are cut show ant injury. The nests are usually built comparatively near the base of the trees, the highest being not much more than 8 or 10 feet above the ground. The exact location of a nest can be determined by the position of the "windows."

Much unavoidable loss is occasioned by ant injury to cedar. It has been estimated that in trees grown on swampy ground there is an average unavoidable loss of about 3 feet from the butt of every ant-infested white cedar, whereas on the higher ground the

average loss is almost 6 feet. A part of this loss is, of course, due to butt rot; it is safe to say, however, that an average loss of at least 2 feet from the butt of every ant-infested tree is ascribable to ant injury.

Control of these insects can be secured in several ways. The simplest method is to inject carbon bisulphide, chlorpicrin, or some other fumigant into the nests. Chlorpicrin, however, should not be used on living trees. Buildings should be set upon stone or concrete foundations so that the timbers will be kept dry. Under such conditions, they will not usually provide favorable nesting places for these insects. In the forest, the ants gain entrance to the trees only through injuries. Fire scars, ax marks, and other surface injuries should be eliminated as far as possible in order to prevent both wood rots and the entrance of ants.

Friend (1937), as a result of experiments in Connecticut, recommends the control of carpenter ants in poles by injecting a mixture of gasoline and coal-tar creosote into the nests. This is accomplished by boring through the upper part of the nest and injecting the material with a grease gun.

Insects Eating Moist Wood.—The pole borer, *Parandra brunneae*, is another insect that is a frequent pest of wood that is not too dry. It is widely distributed probably occurring in all the parts of the United States and Canada that are wooded with hardwood trees. The larvae are elongate, cylindrical grubs like the other round-headed borers in appearance. The adults are glossy, chestnut-brown beetles about ¾ inch in length.

This borer attacks posts, poles, and the dead heartwood of standing trees of many different species of hardwoods. They are found so frequently in chestnut trees that they have been called the *chestnut pole-borers*. Even though this insect attacks living trees, it cannot be regarded as a primary species, because it can gain entrance to such trees only through wounds, and then usually works only in the dead heartwood. Thus a tree is in very little danger of injury by this insect as long as it is in a healthy, vigorous condition. The pole borer is usually associated with organisms of decay. It usually confines its activities to the lower parts of tree trunks or to the portion of a post or pole near the ground line.

The adults emerge in late July and during August and soon thereafter begin their oviposition. The females place their eggs in niches cut into the surface of dead wood or in the walls of old galleries. One egg is laid in each niche. In from 2 to 3 weeks the young larvae hatch, whereupon they take up their labors as wood borers. They tunnel through the heartwood and to a lesser degree in the sapwood making irregular tortuous galleries that may be several feet in length. As they progress through the wood, they pack the frass and sawdust behind them in the gallery. Many larvae usually work together in a limited area, with the result that the entire heart of the tree or pole, at the point attacked, may be hollowed out. It is not usually very long until organisms of decay join the pole borer in its pernicious work, after which they work together until the tree or pole becomes so weakened that it breaks off at the point of attack. It is probable that the larvae require at least 3 years for their full development. When the larvae are full grown, they hollow out pupal cells in the wood where they transform to pupae and later to adults. The adults cut their way to the outside.

The attack of this insect upon poles and posts can be prevented, at least in part, by treating the butt ends with creosote. The treatment, if it is to be effective, should extend a foot or more above the ground. When a pole is once attacked, it is practically impossible to free it of these insects. In standing trees, likewise, the best control is prevention. Avoid wounds of any kind, for it is only in such places that the pest can gain a foothold. Valuable shade or orchard trees that are infested may be treated successfully by surgical methods. If the infested parts are carefully cut out, and the resulting cavity properly filled, the injury can be checked. Surgical work of this kind is expensive and, unless carefully done, may prove worse than useless.

Termites or White Ants.—Another important group of insects that feed on wood are the termites or white ants. The greatest damage caused by them is to seasoned wood in buildings, posts, poles, ties, and fences where the wood is more or less moist as a result either of contact with the soil, some other source of moisture, or the activities of the insects themselves. Sometimes termites may also work in living trees, but this is not especially important outside the tropics (Fig. 123).

The name *ant* as applied to termites is a misnomer, because these insects are not ants at all but are members of the order Isoptera. The termites are, perhaps, the most destructive of all wood-boring insects in the tropics. In temperate lands, however, they are much less numerous and destructive, but they may occasionally be serious pests as far north as the latitude of New York City. Serious trouble caused by these insects has been reported from as far north as Connecticut, Massachu-

FIG. 123.—Galleries of a dry-wood termite in wood. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

setts, New Hampshire, southern Michigan, southern Minnesota, and from the north Pacific Coast states.

The termites, like other insects that eat wood, are faced with a difficult nutritional problem. The material that they eat is chiefly cellulose and is one of the most difficult of the organic substances to digest. The relation of wood-boring insects to wood-rotting fungi has already been mentioned, and it seems possible that these organisms are also helpful in termite nutrition. But nutritional studies with termites have shown that many of

these insects are provided with an intestinal fauna of Protozoa that is directly responsible for the digestion of the cellulose that the termites eat. Without these protozoa, which are provided with cellulose-digesting enzymes, the insects will starve even though they continue to injest wood. How general such a symbiotic relationship as this may be among wood-eating insects is not known, but it may reasonably be suspected of being rather general.

Ecologically the termites of the United States may be divided into three groups on the basis of habits. The dry-wood termites, Kalotermes, live in relatively dry wood without any soil contacts being necessary. The moist-wood termites, Zootermopsis, are also wood termites but usually require that the wood in which they work be moist. The third group, the subterranean termites, of which the genus Reticulitermes is most widely distributed and important in the United States, constructs their nests in wood in contact with the ground.

Fig. 124.—Work of subterranean termites. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

The dry-wood termites are limited in their distribution in the United States to a belt along the Atlantic and Gulf coasts from the southern tip of Virginia to Texas and westward along the Texas and Mexican borders to California and northwest to San Francisco. They attack buildings, posts, poles, fences, and other wooden structures. The moist-wood termites are found mostly on the Pacific Coast, where they attack wood that is moist, usually as a result of contact with the ground. The subterranean termites are by far the most destructive group, and species of Reticulitermes may occur from the subtropics to Canada.

Space will not permit a detailed consideration of all the various species of termites that occur in the United States. Therefore the following discussion is rather generalized. For more detailed information the student is referred to literature cited in the bibliography.

Termites are social insects somewhat ant-like in appearance and live in colonies composed of a number of castes. Each caste has a more or less specific function, and each will be mentioned

FIG. 125.—Winged termite adults, *Reticulotermes virginicus*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

in the following discussion of their biology. The primary reproductives, usually called *kings* and *queens*, are the only members of the colony that at any time have functional wings (Fig. 125). These dark-colored, long-winged males and females swarm out of the nest at certain periods of the year for the purpose of mating and establishing new colonies. The common termite of the East, *Reticulitermes flavipes*, swarms early in the spring. After a brief period of flight they break off their wings and the individual pairs that survive this hazardous period seek out a suitable location for a new nest.

The nests of the subterranean termites are established in wood on or in the soil, whereas the dry-wood species seek out a check, a knothole, or other opening, or may burrow directly into more or less dry wood.

Eggs are deposited and cared for in the new nest. In the case of the dry-wood and moist-wood termites, some of the nymphs

that hatch from these eggs may develop into soldiers. These are individuals with especially large and powerful mandibles whose function is the defense of the nest. Other individuals may develop into winged sexuals, and still others into supplementary reproductives. The last are produced to take the place

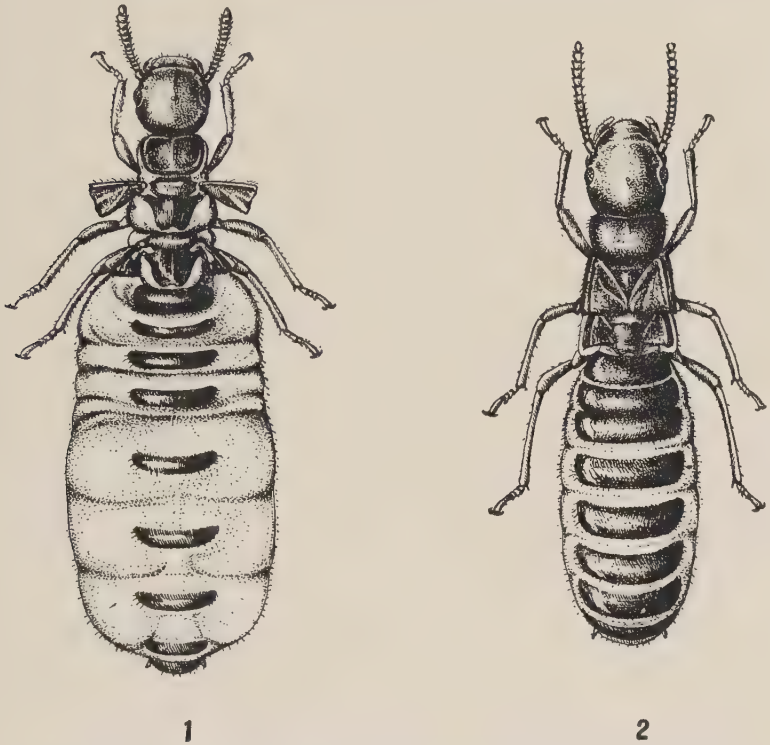


FIG. 126.—Adult termites greatly enlarged. 1. Gravid female with segments distended. 2. Male. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

of the primary sexuals and may arise when the true king or queen dies, or when a part of the colony becomes separated from the parent colony. In the case of the termites moist-wood and dry-wood the bulk of the population consists of nymphs, the laboring caste in established colonies of these termites (Fig. 126).

The subterranean termites differ from these others in that the majority of the nymphs develop into wingless workers, which comprise the laboring class, and these, with the soldiers, make

up the major part of the colony. A smaller proportion of the nymphs develop wing pads and later become winged males and females. In addition to the nymphs that develop into winged adults there are others with shorter wing pads or without wing pads, which may develop into supplementary reproductives. This occurs in large colonies or when part of a colony becomes separated from the rest. According to Pickens (Kofoid, 1934) these supplementary reproductives in the case of the Western subterranean termite, *Reticulitermes hesperus*, develop more rapidly than the primary reproductives, are at least as prolific individually, and may live peaceably together several in a cell. Thus their presence speeds up materially the growth of a colony. He points out that the growth of the primary colony is very slow, and accounts for the rapid infestation of buildings by the combination of several primary colonies, the elimination of all but one pair of primary reproductives, and the development of many supplementary reproductives.

Termites may sometimes be in a building a long time before making their presence known by swarming, or by the failure of the timbers weakened by their mining. Their activities are mostly within the wood, but careful inspection will often reveal the presence of fecal pellets thrown out of the nests by the dry-wood termites, or the exploratory or bridging passages of the subterranean species.

The subterranean termites always enter wooden structures from the ground, where the nest is located. The nest may be in a tree stump, in pieces of waste wood buried near the foundation or under the building, or in other similar wood materials. From these nests the termites construct tunnels through the ground and covered passages over foundation walls and other objects through which they cannot tunnel. Thus their injurious work may be some distance from the nest. They must, however, maintain a continuous contact with the soil. The loss of such contact is fatal.

Therefore the best way to protect wooden structures from the attack of subterranean termites is to build in such a manner as to separate effectively the untreated wood from the soil by solid, good-quality concrete or metal. Detailed specifications for the termite-proofing of buildings will be found in references cited in the bibliography. In general the following points should be observed:

1. Clean up all waste wood under and about buildings and remove all stumps before grading.

2. Set buildings on concrete foundations at least 18 inches above the ground, using a good cement mix either for a poured wall or for laying up a stone or block wall.

3. Cap foundations with a metal termite shield.

4. Use a good cement mix for basement floors and close expansion joints with pitch or metal.

5. Keep all untreated wood away from contact with the ground.

It is advisable although not essential to use sills that have been effectively treated against termites, or sills of a resistant species like redwood, southern cypress, or the heartwood of longleaf pine. Some resistant tropical woods are, according to Snyder, teak, sal, camphorwood, and cypress pine.

The best time to control termites in a building is at the time of construction. If, however, a building becomes infested, steps must be taken to construct a physical or chemical barrier or both between the nest and the infested wood. Also nests and potential nesting places near the building should be destroyed.

A number of materials may be used in treating wood to protect it against the attack of termites. One of the most satisfactory and effective methods is pressure treatment with creosote. Brush treatments give some protection but are by no means so certain as the pressure method.

Termites seem to be increasing in abundance in the north and central parts of the United States and it is often felt that they are extending their range northward. This may be true, but it seems more probable that modern styles in residence architecture that demand very low foundations may be a stimulus to the multiplication of these insects and the northward spread may only be apparent. Another factor of importance in causing these insects to increase may be indirectly associated with the use of steam shovels for basement excavations. This method of excavation usually leaves a large space in the ground outside the foundation wall into which wood waste inevitably falls during construction. There is a tendency on the part of builders not only to leave this wood in the trench but also to throw in other waste material, knowing that it will be effectively hidden by grading. In this way ideal conditions for termites are created

next to the foundation. Obviously such practices are undesirable and should not be permitted.

MARINE WOOD-BORERS

The wood-boring insects are so numerous, and their work is so conspicuous and so familiar to everyone, that we are sometimes prone to think only of insects when we consider wood-boring organisms. As a matter of fact, however, wood provides food or shelter for many other forms of life. Among the most important of these, from the economic standpoint, are the marine borers. In the strictest interpretation of the scope of forest entomology these organisms would be excluded, but inasmuch as they are often thought to be insects by the layman, and inasmuch as they are responsible for tremendous losses wherever wood is used in salt water, it seems appropriate that at least a brief discussion of them should be included here. The most destructive of the marine wood-borers are the bivalve mollusks called *shipworms*. Much damage also results from the activities of several genera of marine crustaceans called *wood lice*. The most common genus of these crustaceans is Limnoria. Each of these will be considered in turn.

The Shipworms.—The shipworms, Bankia and Teredo, have been known to maritime peoples since the dawn of history and have been studied periodically from earliest times. When we consider the time that has been spent upon the study of these creatures by investigators in centuries past, it is surprising that we know so little about them. The imperfect state of our knowledge concerning this group is emphasized by the statement of Bartsch, published in 1922, to the effect that " . . . the complete life history of not a single species is known today." Although much more information has been accumulated since this statement was made, especially on the Pacific Coast, much more remains to be learned. It is not surprising, therefore, that methods used in the control of these pests are not entirely successful.

In the past, it was thought that there were only a few species of shipworms and that these were practically universal in their distribution. It has now been shown that many species exist and that, for the most part, each one is definitely limited geographically, just as terrestrial organisms are limited to definite

ranges by ecological factors. Bartsch, in his "Monograph of American Shipworms," lists 30 distinct species that inhabit the waters of the Western Hemisphere.

Shipworms attack all kinds of wood. Very hard woods are somewhat resistant but are by no means immune to attack. It is said that very soft, porous woods, like palmetto, are not very attractive to shipworms but nevertheless are attacked. In fact, shipworms will attack any wood that is submerged in salt water. The greatest damage is done to piling. The replacement cost of piling destroyed annually by these animals is tremendous. The following table will give some idea of the rapid destruction of piling that may occur in warm salt water.

LIFE OF PINE PILING IN DIFFERENT LOCALITIES*

Locality	Length of life in months	
	Average	Minimum
Colon, Panama	10	
Norfolk, Va	60	12
Newport News, Va	24	
Hampton Roads, Va	18	
St. Andrews, Fla	30	
Pensacola, Fla	30	12
Fort Morgan, Ala	..	12
West Pascagoula, Miss	30	12
Texas City, Tex	12	1
Galveston, Tex	18	5
Aransas Pass, Tex	12	3
Puget Sound, Wash	12	
Klawak, Alaska	36	18

*Smith, U. S. Dept. Agr., Forest Service, Cir. 128.

As will be seen upon examining the preceding table, the injury by shipworms is greater in warm water than it is in cold. On the Atlantic Coast the pest is not serious north of the Chesapeake Bay, although some species are able to live as far north as the Maine coast. On the Pacific Coast the warm waters of the Japan current make conditions favorable for them as far north as Alaska. Temperature, however, is not the only limiting factor in the life of these animals. Salinity of the water in which they are living has a decided influence upon them. Fresh water is decidedly

detrimental; this probably explains the comparatively long life of piling at Norfolk, Va.

The shipworms in early life are free-swimming organisms and are provided with a bivalve shell. After certain stages have been passed in the water, the young mollusks attach themselves to submerged wood. They bore into the wood leaving very small openings to the outside. Under favorable developmental conditions a pile may be attacked by thousands of these tiny creatures. Once inside the wood they grow rapidly and enlarge the tunnel to suit their increased size. The shell is used as a

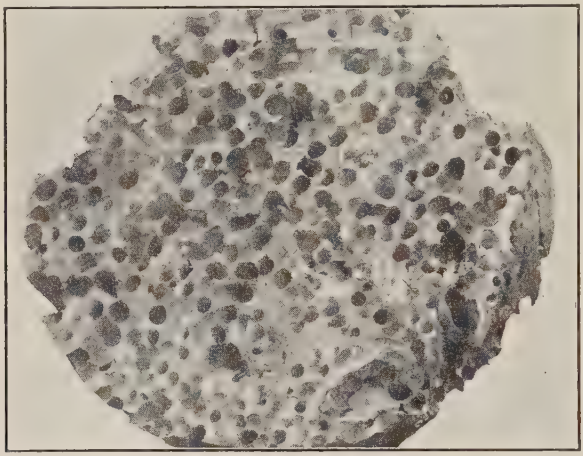


FIG. 127.—The work of shipworms in a douglas-fir pile. The wood has been almost completely destroyed by the burrows of these animals. (*University of Minnesota.*)

boring tool and is no longer needed for protection of the body. The animal, in its burrow, is elongate and soft bodied, with the small chisel-like shell at the anterior end of the body and, at the posterior end, two tubes that are the exhalent and inhalent siphons. Some of the larger species of shipworms may attain a length of 4 feet, under favorable conditions, while other species may never exceed 5 inches in length. As the shipworm develops within its tunnel, it secretes a calcareous, shell-like material which is used to line the burrow (Fig. 127). This shell-like lining is thicker in soft porous woods and thinner in harder woods.

Considerable diversity of opinion has been expressed concerning the food of the shipworms. Some authorities maintain that the wood passes unchanged through their digestive tract,

and that their entire food consists of plankton drawn in through the inhalent siphon. Recent work by several investigators has demonstrated, however, that this is not true. Although plankton probably forms a considerable part of the shipworm's diet, recent workers have shown that 80 per cent of the cellulose, and from 15 to 16 per cent of the hemicelluloses, contained in a douglas-fir pile were lost during the passage of the wood through the digestive tract of *Teredo navalis*. Furthermore, the proportion of reducing sugars was much higher in the caecum of *Bankia setacea* than in the original wood (Dove and Miller, 1923; and Miller and Boynton, 1926). From these observations, we must conclude that at least a part of the wood that passes through the digestive tract of these animals is digested and assimilated.

Owing to the fact that the entrance hole into the wood is very small and inconspicuous, there is usually little indication externally of the presence of the borers. More than one-half of the volume of a pile might easily be destroyed without any evidence of injury being apparent on the surface. Only by cutting into the pile can its condition be ascertained. The portion of a pile that is most susceptible to shipworm injury is that between mean tidewater mark and about 4 feet below low water. The entrance holes are usually in this portion of the pile, although the active boring may be several feet above or below the point of entry.

Control of shipworms is, theoretically, a simple matter, but, practically, it is anything but simple. Protecting the susceptible parts of piling with any sort of covering will prevent the attack of these pests. Metal sheathing of copper, iron, or any other metal is effective but expensive, and not very durable owing to the corroding action of salt water. Cement casings of various kinds have been suggested and experimented with, but have not proved satisfactory because of cracks that are almost certain to develop as the result of expansion and contraction, or of wave action, or the battering of driftwood. Likewise, coatings of tar, asphalt, pitch, and other similar materials give protection while they remain intact, but a single blow from a piece of floating debris may easily open the way for infestation. Unbarked piling is not susceptible to shipworm attack while the bark remains intact, but it is next to impossible to find a stick with no break in the bark. The success of all these mechanical-barrier methods of protection depends upon the maintenence of an unbroken

covering. The smallest break in the protective covering opens the wood to an attack that may easily result in the complete destruction of the pile. The only really successful method of protecting piling against shipworms that has been developed so far is impregnation with creosote. Surface treatment is not sufficient. Only by pressure treatments, or by alternate hot- and cold-bath treatment, can the wood be sufficiently impregnated to resist attack. Satisfactory impregnation is impossible to obtain

FIG. 128.—Work of the wood louse, *Limnoria sp.* Each hole is the burrow of an individual crustacean.

with dense hardwoods; therefore only pine, douglas fir, or other porous softwoods should be used.

Movable structures and boats may be protected by an unbroken covering of paint. When borers have gained entrance into wooden vessels they can be killed by running the boats into fresh water.

The Wood Louse.—The wood louse, Limnoria, is another of the marine borers that does considerable damage along the Atlantic Coast (Fig. 128). It is confined to clear salt water and cannot endure fresh or turbid water. Its temperature range is much greater than that of the shipworms and, as a result of this, it is found much farther north. It is very common along the New England coast and in the Bay of Fundy.

The wood louse is a crustacean only about $\frac{1}{8}$ inch long and suggests in form a very small sow bug. Limnoria is gregarious and attacks piling and other structures in large numbers, usually near low-water mark. As a general rule, the greater the differ-

ence between high and low tide, the greater will be the vertical distribution of these organisms.

Limnoria finds both food and shelter in the wood that it attacks. Each individual gallery is short, about ½ inch in length, and penetrates directly into the wood. When large numbers attack a pile, their tunnels almost touch so that the thin walls between them are quickly worn away by wave action, leaving a new surface of wood ready for reinfestation. The progress of this injury is slower but more easily seen than the work of the shipworms. Heavily infested piling may lose 1 inch a year in diameter as a result of Limnoria attack. The control of Limnoria may be accomplished by impregnating with creosote wood exposed to salt water.

DRY-WOOD INSECTS

In the preceding sections of this chapter, those insects and other animals that usually attack moist wood have been studied. Now we come to a group of insects that are able to attack sound, dry wood. There are comparatively few groups of insects that are able to live throughout their entire developmental period in this medium. It has been a constant question to entomologists how any insect can digest sterile wood. This has now been explained for the termites, as we have already seen, by the presence of an intestinal fauna capable of digesting cellulose, but it has not been demonstrated for most other wood eaters. It seems likely that this symbiotic relationship may be characteristic of most if not all of the dry-wood insects.

The Powder-post Beetles.—The name *powder-post beetle* is applied to representatives of several small families of the Coleoptera that feed upon dry wood. The two families that contain most of the powder-post species are the Bostrychidae and the Lyctidae. In America, the species of the genus Lyctus are the most common insects of this group. *Lyctus planicollis*, *Lyctus parallelopipedus*, and *Lyctus cavicollis* are three common species of these beetles.

The beetles of this group are called *powder-post beetles* because of their effect upon the wood in which they work. They may reduce the entire interior of a piece of wood to a fine, flour-like powder, leaving only the exterior shell intact. These beetles are pests of the sapwood of broad-leaved trees. Wood of oaks,

hickories, ash, and poplars are frequently injured. Since the heartwood is immune, the injury is always confined to the sapwood.

The powder-post beetles feed only in dry, well-seasoned wood. As a rule, a full year of air drying is required before the wood becomes suitable to the taste of these beetles, although small

FIG. 129.—A hickory shovel handle destroyed by powder-post beetles.

pieces may dry out more rapidly and become susceptible to attack in 8 months after cutting. Kiln-dried material is susceptible to attack as soon as it leaves the kiln.

One full year is required to complete the life cycle of these insects. The adult beetles emerge in the early spring, and it is at that time that the injurious work of these pests is most likely to be noticed. It is not at all uncommon during the spring months for dealers in such hardwood products as handles and wagon or automobile stock to discover that they have been harboring, unaware of their presence, these unwelcome guests (Fig. 129). Sometimes, when infestation is severe, a merchant's entire

supply of ax and shovel handles may be destroyed before he realizes that the insects are present. Occasionally, infested flooring may be laid and finished without anyone realizing that the wood is not perfectly sound, and it is not until the beetles emerge in the spring that their presence is recognized. Even furniture may be infested. When this occurs it usually happens before the wood has been finished. Until they emerge as adults, there is often no sign of the infestation. Then the wood may be peppered with the small, round, exit holes which the beetles

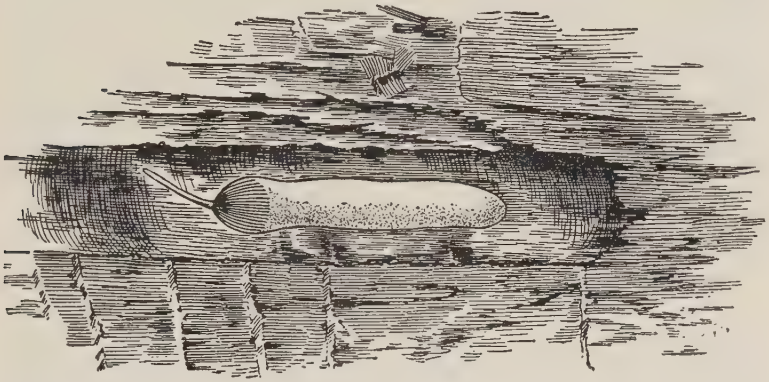


FIG. 130.—An egg of a lyctus beetle inserted in a sapwood pore. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

have cut to the outside. Fine, powdery borings, previous to or at the time of emergence, are another indication of infestation.

During the brief period of flight in the spring, mating takes place and the females seek out suitable places for oviposition. The eggs of the lyctus powder-post beetles are laid in pores of the sapwood (Fig. 130). When the young larvae hatch from these eggs they find themselves in a desirable location and immediately proceed to make the best of their opportunities. Their first meal consists of the remains of the eggs from which they hatched, but from then on they must find sustenance in the solid, dry wood. The larvae cut irregular winding galleries in the wood. As they progress, they pack the finely pulverized frass behind them in the tunnel. The winter is passed in the larval stage. In early spring the transformation, first to pupae and next to adults, takes place within the wood. The adult beetles then cut their way to the outside in order to emerge.

Prevention is the keynote of powder-post-beetle control, because after wood is once infested by these insects it is usually fit for nothing more than firewood. In lumberyards and manufacturing plants, where large quantities of hardwood stock must be kept on hand, thorough inspection of wood more than 1 year old should be made annually for the purpose of eliminating any stock that may have become infested. The best time for inspection is in the winter months. Infestation is usually indicated by small quantities of fine borings that sift out of infested pieces. Infested pieces break easily, exposing the powder-filled tunnels to view.

In order to simplify inspection, heartwood and sapwood stock should not be piled in one pile. The heartwood is not susceptible and need not be inspected, hence separate piles of sapwood and heartwood would reduce the labor of inspection. Wood in storage should also be classified according to age because the oldest wood is most likely to be infested. All new stock should be carefully inspected to prevent introducing the beetle into uninfested sheds and storehouses. Any suspicious material should be kept under observation for several months.

Rapid utilization will greatly reduce the chance of infestation in storage sheds inasmuch as wood that is less than 1 year old is never a menace. Wood kept on hand for several years is likely to become a great danger if it becomes infested. Wood-working industries should always utilize first the oldest stock on hand. All waste sapwood should be burned or hauled away from wood-working establishments; under no circumstances should it be allowed to accumulate or else powder-post beetles may become established in these waste piles and from there infest the stock piles.

Ordinarily the safest course of procedure in dealing with infested material is to burn it. Sometimes, however, a part of the stock that has not been too heavily injured may be saved if the insects working in it can be killed. To accomplish this, the dipping of infested wood in kerosene or in orthodichlorobenzene has been recommended. Repeated applications of either of these materials to infested wood, by means of a brush or a spray, will kill the insects. Both of these materials will evaporate, leaving the wood unstained. Dipping in a mixture of hot kerosene and creosote has also been recommended. This, however, discolors the wood.

In using hot inflammable oils such as kerosene, it should be borne in mind that to heat liquids of this sort over an open flame is to invite disaster, since a fire or an explosion is almost certain to be the result. Inflammable oils should always be heated by steam coils arranged in the bottom of the dipping vat.

One of the most effective means of protecting susceptible wood from the attacks of powder-post beetles is by treatment

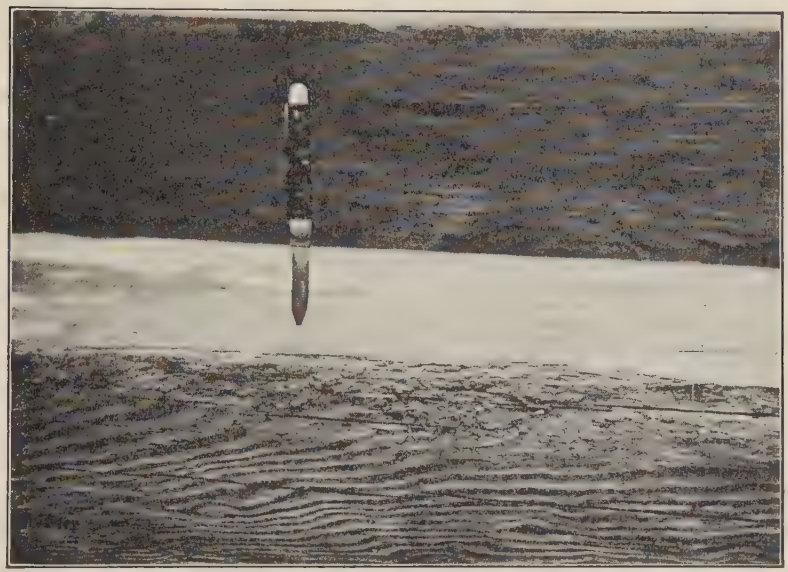


FIG. 131.—A piece of wood in which the unpainted portion was attacked by powder-post beetles while the painted and varnished portions, behind the knife, remained unattacked. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

with boiled linseed oil, varnish, or paint (Fig. 131). It will be remembered that the lyctus powder-post beetles deposit their eggs only in open pores of wood. Treatment with any of the materials mentioned above will close the pores and prevent oviposition by the beetles. In many lumber yards it is customary to paint the ends of hardwood lumber to prevent checking. This treatment also protects the wood against end attack by powder-post beetles. It does not, however, prevent side attack.

CHAPTER XV

SAP-SUCKING INSECTS

All the insects discussed in the preceding sections feed upon the tissue of trees by ingesting the solid parts. All of them have mandibulate mouth parts. In addition to these chewing insects, there is a large and important group the species of which live upon sap. Their mouth parts are of the sucking type in which the mandibles and maxillae have become slender, bristle-like organs enclosed in a sheath, the labium. This forms a beak which is used for the purpose of piercing tissues and sucking the juices therefrom. The sucking insects that attack trees belong to two orders, the Hemiptera and the Homoptera. Both of these orders contain families that are exclusively phytophagous.

The effect of sucking insects upon trees is much less conspicuous than is the effect of defoliators, meristem insects, or wood borers. The insects of this group seldom kill trees directly, but they may, nevertheless, have a distinctly injurious effect upon the forest. Because their work is not conspicuous, most of the sucking insects of forest trees have received comparatively little consideration. On orchard and shade trees, on the other hand, they are acknowledged to be exceedingly important enemies. As the intensity of forest management increases, the importance of these species in the forest will doubtless receive increasing recognition, for, unquestionably, the sucking insects do as much actual damage to forest trees as they do to orchard and shade trees.

Sucking insects may injure plants in two ways: first, directly, by sucking the sap and thus robbing the plant of a part of its supply of food and water, and second, indirectly, by disseminating plant diseases. It has been shown in the case of woody shrubs, such as raspberry, and also in the case of many herbaceous plants that some of the so-called physiological diseases are really caused by disease organisms that are carried by sucking insects. In some instances, the insect may serve in the capacity of an intermediate host for the disease. The mosaic diseases are transmitted from

plant to plant by sucking insects, and, in some cases, this is the only way that these diseases can be carried from one host to another. How important the insect-borne diseases may ultimately prove to be in forests, time alone can tell.

Many sucking insects may also injure trees mechanically, by ovipositing in them. In fact some species, for example, certain tree hoppers (Membracidae), do not generally feed upon trees at all, but they still may seriously injure or even kill trees by filling the branches with their egg slits (Fig. 132).

The species of sucking insects that attack trees are so numerous that space will not permit a full consideration of this important group. The discussion will be confined to a few representative types of the more important families.

FIG. 132.—Scars on an aspen twig caused by the oviposition injury of tree hoppers.

HEMIPTEROUS INSECTS

The order Hemiptera embraces a large number of sucking insects. The members of this order are the true bugs, and it is only to this group that the name *bug* can be correctly applied. A number of Hemipterous families are predaceous, some of them upon forest insects, but it will be necessary to pass them by and confine the discussion to those that suck the sap of trees.

The Plant Bugs.—The members of one family of the Hemiptera, the Miridae, are known as *plant bugs* and contain many tree species. Every tree of every species is infested with its share of these insects, but they seldom occur in sufficient numbers to be recognized as injurious pests of forest trees. A few of them, like the tarnished plant-bug, *Lygus pratensis*, and the box-elder bug *Leptocoris trivittatus* (Fig. 133), are sometimes injurious in nurseries. The eggs of these insects are deposited in slits which the females cut in the twigs and small branches of trees. The young that hatch from these eggs bear a decided resemblance to the adult, except that they have no wings. They run about actively and get their food by puncturing the leaves or stems

and sucking the sap. The metamorphosis of these, like all other Hemiptera, is gradual. With each succeeding molt, the nymphs become more and more like the adult until the final molt, when they appear as winged imagos. No satisfactory control for these insects has ever been developed. Even when occurring on nursery stock and fruit or shade trees they defy control. They are resistant to contact sprays and their method of feeding precludes the possibility of killing them with a stomach poison.

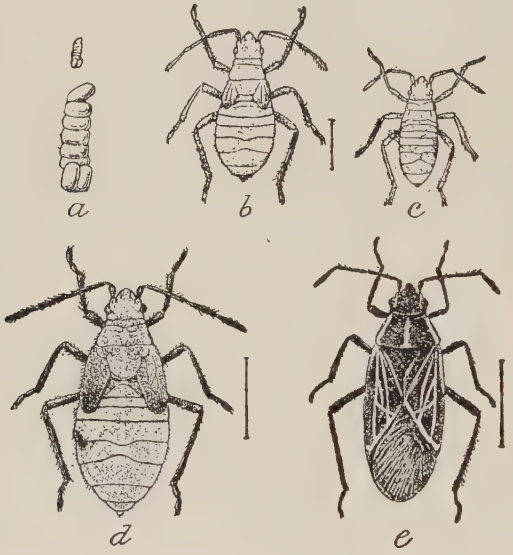


FIG. 133.—Various stages of the box-elder plant bug, *Leptocoris trivittatus: a.* eggs; *b, c, d.* nymphs; *e.* adult. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

The Lacebugs.—Another important family of the Hemiptera is the family Tingidae, the lacebugs. These insects are very small in size, usually not much over $\frac{1}{8}$ inch in length, but they are nevertheless very striking in appearance. The hemielytra are thin, almost gauze-like in structure and are marked by a network of fine lines that give the insect a lace-like appearance. Lateral expansions of the prothorax that are similar in structure and appearance add still more to the lace-like effect (Fig. 134).

Unlike the leaf hoppers, which are very active in all stages, the lacebugs lead a sedentary life. Their entire developmental period may be spent upon a single leaf. Injury done by them is

much more likely to be observed than that caused by the plant bugs, in part because it is usually more localized, and in part because the insects themselves are more easily seen.

The lacebugs sometimes occur in extremely large numbers and in some years may destroy over extensive areas practically all the foliage of their host trees. They are not, however, tree killers. They attack trees of all sizes, but appear to prefer trees of sapling or small-pole size. Drake (1922) considers one of the tingids, *Corythuca pallipes*, to be "the most injurious leaf-feeding insect on yellow birch" in certain parts of New York State. These insects are sometimes very seriously injurious to hardwood trees growing in nurseries. The birch is one of the common hosts for a number of lacebugs, but other hardwood species (for example, ironwood, sycamore, oak, maple, willow, and basswood) are often heavily attacked.

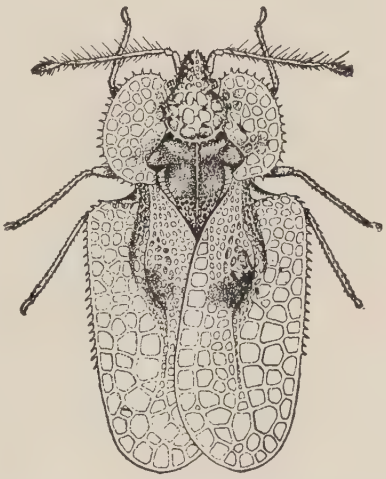


FIG. 134.—The sycamore lacebug, *Corythuca ciliata*. Adult, greatly enlarged. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

The life history of the lacebugs is in some ways quite similar to that of other Hemiptera. The eggs are deposited on the underside of leaves of the host tree, usually in the veins. Each egg is inserted partly in the leaf tissue, sometimes singly but usually in groups. No definite method is followed in arranging the groups. The eggs are dark in color, rather elongate, and slightly curved in form, with the upper end somewhat constricted and closed with a lighter colored cap or lid. They hatch in about 10 days after deposition.

The young nymphs that hatch from these eggs insert their proboscises into the leaf tissues and suck out the sap. During the early nymphal stages they are usually gregarious. When they become mature they generally scatter. The adults feed on both the upper and lower surfaces of the leaves, whereas the nymphs practically always feed only on the lower side.

Almost all the lacebugs have two generations a year in the latitude of New Jersey. It is probable that farther north they may have only a single generation, while in the South they may have more. Most of the species pass the winter in the egg stage, although a few become adults before hibernation. These overwintering adults hide themselves away beneath bark, or in the litter beneath the trees, or in any other sheltered location.

The control of lacebugs in nurseries and on shade trees can be accomplished with comparative ease. Spraying with a contact insecticide is usually effective. On lawn trees the insects may be held in check by washing the foliage thoroughly with a forcible stream of water from the garden hose. Whale-oil soap at the rate of 1 pound to 6 gallons of water has been recommended. In spraying for these and other sucking insects, it is important that the spray be applied with considerable force. This means that with a 50-foot lead of hose a pressure of 200 to 250 pounds should be maintained at the pump.

CERTAIN HOMOPTEROUS INSECTS

Many members of the order Homoptera are important enemies of forest and shade trees; in fact almost every family of the order has representatives that feed upon trees. The most important groups, from the viewpoint of forest entomology, are the aphids or plant lice, the adelgids, and the scale insects, but members of other families are sometimes important locally. For instance, the cicadas, although they do little damage to the tree during their long, subterranean, developmental period during which they feed upon tree roots, sometimes cause heavy injury to shade and nursery trees at the time of oviposition. Certain species of leaf hoppers are primarily tree insects. The tree hoppers feed on both woody and herbaceous vegetation and sometimes severely injure or even kill trees in which they oviposit heavily. This injury is particularly common in nurseries and in the farm windbreaks and groves of prairie regions. The froghoppers or spittle bugs injure and sometimes kill pines when they attack these trees in large numbers. The chermids or jumping plant lice are particularly injurious to orchard trees, sometimes even killing them. The members of these families, however, in spite of the fact that they sometimes are injurious, cannot be regarded as

forest pests of primary importance. A detailed discussion of most of them will, therefore, be omitted here.

The Periodical Cicada.—In addition to the aphids, the adelgids, and the scale insects, we shall discuss here a representative of only one other of the Homopterous family. That is the Cicadidae. The more common species of this family are well known to almost everyone, for those who do not know the insects by sight are familiar with the strident, rattling song of the male that is so characteristic of warm summer days. They are called *harvest flies* and sometimes incorrectly termed *locusts*. One

FIG. 135.—An adult of the periodical cicada, *Magicicada septendecim.* (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

of the most injurious and best-known members of this family is the periodical cicada, *Magicicada septendecim;* this species will serve well as a representative of the group (Fig. 135).

The periodical cicada appears from time to time in great swarms, particularly in regions of Eastern North America that are heavily wooded with hardwood trees. The female lays her eggs in slits that she cuts in small twigs and branches of woody plants. When the cicadas occur in great numbers, every available twig may be filled with egg slits, with the result that many twigs will be killed. This is not particularly injurious to mature forest trees, but to young trees in the forest or the nursery it may be disastrous (Fig. 136).

The periodical cicada has an astonishing life history which is, indeed, stranger than fiction. The full-grown nymphs, sometimes called *pupae*, emerge in spring and early summer from the ground where they have been entombed while passing through

FIG. 136.—Injury to the small branches of hardwood trees caused by the oviposition of the periodical cicada. On the left recently injured twigs are shown. On the right are old injuries, healing over. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

the developmental stage. In certain years, they appear in such quantities that large areas of ground from which they have emerged are literally peppered with their exit holes. In some places, 50 to 100 exit holes per square foot of soil surface are not uncommon.

The full-grown nymphs are curious, heavy-bodied insects with a broad, blunt abdomen, and powerful legs. As soon as they leave their burrows, they climb upon any convenient object and there hook their claws firmly into the supporting surface and come to rest. Before very long, a split appears along the back of the thorax and the adult emerges, leaving the empty nymphal skin hanging where it was fastened. Trees, shrubs, fences, poles, and any other convenient objects, in years when cicadas are abundant, may be covered with these cast skins.

The adult, when fully pigmented, is dark brown to black in color, with red eyes. When the insect is in a resting position, the clear, membranous wings are folded over the body like a tent. The head and thorax are broad, and the abdomen is tapering. The females are each armed with a strong ovipositor that might appropriately be compared to a pair of chisels. By means of this powerful tool they gouge out slits in twigs and small branches in which to deposit their eggs. The height of the oviposition period usually comes in June. The period of incubation is long, requiring 6 or 7 weeks. When the young nymphs break from the eggs they drop to the ground and promptly burrow downward into the soil.

There, at a depth of about 2 feet, they hollow out an earthen cell next to one of the small roots of some tree or shrub. The insect then inserts its beak into the tissues of this root and proceeds to suck the juices therefrom. This liquid food provides the only nourishment for the insect. The periodical cicada grows very slowly. Safe in the seclusion of its earthen cell, there is no need for haste in completing its development. The slight mechanical injury to the root resulting from the insertion of the cicada's beak is of little consequence; therefore the root provides for the nymph a regular and certain source of food which will continue for an indefinitely long period. Thus, unlike most insects, the length of life of the nymph is not limited by changing food conditions. The combination of a readily available, permanent food supply with a habit of life that gives the insect

almost perfect protection from its enemies makes possible an exceedingly long developmental period. The periodical cicada lives for 17 years in the nymphal stage. This is the longest life cycle known for any sucking insect.

Most other insects which have long life cycles have overlapping broods, some of which emerge each year. This is not so with the periodical cicada. One season all the individuals of a brood emerge simultaneously in a locality. The insect may then be so abundant as to be a veritable scourge. In the following years not a single specimen of the insect will be found and not until the seventeenth year will they again appear. In some localities, however, there may be more than one brood. The adults of the several broods need not emerge at the same time, but the generations of every brood are, without exception, always separated by seventeen years. The broods of this insect are well known to entomologists. Each one is numbered and the time and geographical distribution of each emergence can be prophesied exactly. In the South, there is a race of this species which has a somewhat shorter life cycle. Only 13 years is required for its development. It is thought by some that this is a different species, but the general consensus of opinion appears to be that it is merely a biologic variety.

The control of this insect by direct means is virtually impossible. If the branches of trees and shrubs that contain eggs were pruned off and burned before the eggs hatched, the numbers of cicadas could doubtless be reduced. But pruning of this sort is usually out of the question because of the tremendous numbers and general distribution of the eggs.

Natural enemies are important aids in reducing the number of cicadas. Birds, particularly those of the blackbird group, are very fond of the newly emerged adults and consume them by the hundred. The house sparrow and many other birds are said to feed upon this insect. Just before emergence the nymphs come up to the surface of the soil. Here they are sometimes found and destroyed by scratching birds, moles, or hogs.

The Aphids.—Among the homopterous sucking insects the family Aphididae stands out prominently as an exceedingly important group. The members of this family are called *aphids* or *plant lice*. They are abundant in numbers, both of individuals and of species, and they are so generally distributed that it is

scarcely possible to find a tree of sapling size or larger which is not infested by them to a greater or less degree.

The aphids are usually very small, soft-bodied insects. Their bodies are generally pear shaped. The legs are long and slender. With most species, on the dorsal side of the abdomen near the caudal end, there is a pair of cornicles. Aphids may be either winged or wingless. When wings are present, all four of them are transparent, delicate, and provided with a few simple or branched veins (Fig. 137).

Fig. 137.—Aphids feeding on a stem. The individuals that appear to be swollen are parasitized. The emergence hole of a parasite may be seen in the abdomen of the uppermost aphid. A dipterous predator appears on the lower part of the stem.

When aphids occur in comparatively small numbers, the direct injury that they cause is comparatively slight; but when they become very abundant, as they frequently do under favorable weather conditions, their injury to the trees is often great. They are not tree killers, however, and, with the exception of young trees, the injury which they cause usually results only in a reducted rate of growth and in a generally unthrifty condition of the infested trees. Trees injured by aphids may succumb to secondary insects which they could resist when in vigorous health.

Aphids have received much study as agricultural and horticultural pests, but because our forestry methods are decidedly extensive rather than intensive, these insects have received little attention as forest pests. Nevertheless, in view of their abundance, it cannot be doubted that the aphids comprise an important group of forest insects. In nurseries and in young plantations the aphid problem is often exceedingly important.

Occasionally aphids may kill large trees as in the case of Sitka spruce in parts of Oregon and Washington (Keen, 1938) by *Aphis abietina*. Little detailed information concerning forest aphids is available in literature and therefore it seems desirable here to treat the entire family as a unit, rather than to discuss a limited number of individual species.

Different aphids have different habits. Some of them live on the bark of the trunk and large branches, others confine their

FIG. 138.—Galls of the poplar gall-aphid, *Pemphagus populi-transversus*. One of the galls has been opened to expose the interior. (*University of Minnesota.*)

feeding activities to the leaves and green tips, while still others feed upon the roots of trees. Some of them cause the formation of galls, particularly on the leaves. They live within their galls, and thus the tree provides them with both food and shelter (Fig. 138). Other species provide shelter for themselves by causing the leaves on which they are feeding to curl about them. Still others live unprotected on the surface of the trees. Some aphids are provided with glands which secrete a flocculent, wax-like material which collects over the insects and affords them some protection from their enemies and from the weather.

All aphids secrete a sweet material called *honeydew* which is highly prized for food by ants and other insects. For this reason, it is a common sight to see ants among groups of aphids busily collecting this sweet liquid. In some instances interesting symbiotic relationships have arisen between ants and aphids.

Fig. 139.—Aphid eggs on the bark of an oak tree. (*University of Minnesota.*)

The ants care for the aphids and in return receive honeydew. It is because of this relationship that aphids are sometimes called *ant cows.*

Although the habits of the various species of aphids vary greatly, the general features of the life cycle are quite similar for most of the common species. The true aphids pass the winter in the egg stage on the host tree (Fig. 139). In the spring, with the appearance of green vegetation, parthenogenetic females hatch from these overwintering eggs. These females are called

stem mothers. It is from them that the summer generations arise.

The stem mother, or *fundatrix*, as she is sometimes called, is wingless in most species. These young are all agamic females which in their turn reproduce parthenogenetically and are called *wingless agamic* forms or *spuriae apterae.* From these may be produced a number of generations of similar forms, each generation giving birth to living young. Reproduction is very rapid. In from 5 to 7 days after an individual is born, she will, in her turn, begin to produce living young. It is not surprising, therefore, that the aphids build up rapidly in number as the season progresses.

In certain generations another type usually appears. These are winged agamic females and are known as *migrants*, or *spuriae alatae.* Frequently, both winged and wingless forms are present in the same generation. These forms are often produced by the *spuriae apterae* at a time when the food plant has become crowded. In certain species, the migrants are produced directly from the stem mother. These migrants leave the plant upon which they have been feeding to seek fresh food. Some species seek out plants of the same species as that which they left, but a large number of aphids have an alternate host to which the migrants fly. When this is the case, the host upon which the stem mother and the succeeding generations are produced is called the *primary host;* the host species to which the migrants fly is termed the *secondary host.*

On the new host the migrants give birth to winged or wingless agamic forms. A number of generations of these usually occur. On a secondary host the wingless agamic forms may or may not resemble the form on the primary host. Sometimes they are so different that they have been regarded by entomologists as distinct species until a careful study of their life history has disclosed their identity. The members of the last generation of this series give rise to the true sexes and are therefore known as *sexuparae.* In those species that have alternate hosts this generation is winged, at least in part, whereas species which always remain on the same host may be wingless.

The winged *sexuparae* that are to produce the sexually perfect females fly from the secondary host back to the primary host. There they give birth to the oviparous females, which only

appear at this stage in the cycle. The males are usually produced by nonmigrating *sexuparae* on the secondary host and migrate to the primary host. Mating takes place there and eggs are deposited. In some species, each female produces only a single fertilized egg, whereas, in others, several eggs may be produced.

The control of aphids is practically the same for all species. In the forest, no control is practiced, and little thought has been given to this particular side of the aphid problem. There is a possibility that some species that require alternate hosts may ultimately be controlled, in intensively managed forests, by eliminating one of the hosts. But such a development is probably far in the future. For the present, it seems likely that the control of aphids will receive little consideration in established forests. Only in nurseries, in young plantations, and on ornamental trees will they receive much consideration.

In such instances, direct control measures will usually be used. Spraying is the surest and best means of controlling these insects on standing trees. During the growing season, nicotine sulphate in soap solution at the rate of 1 part of nicotine sulphate to 600 or 800 parts, by volume, of strong soapsuds will usually give satisfactory control when thoroughly applied as a spray. The overwintering eggs may be destroyed by a dormant spray of lime sulphur or miscible oil.

Stock that is infested in the nursery should not be set out, either in forest or ornamental plantations, without its first being treated to destroy the aphids. Successful treatment may be accomplished in two ways. The planting stock should either be dipped or fumigated. Dipping is apparently a little more certain than fumigation. Either lime sulphur or miscible oils, at winter strength, will usually give satisfactory results. Another material that is apparently satisfactory for this purpose is nicotine oleate. This material is made by mixing a free nicotine solution with oleic acid, at the rate of 10 parts of a 40 per cent free nicotine solution with 7 parts of commercial oleic acid. It is an effective ovicide when used at the rate of 1 part of nicotine oleate to 40 parts of water.

The Adelgids.—The adelgids (chermes) are close relatives of the true aphids but differ from them in several important respects. For instance, the adelgids have no cornicles, and both the

parthenogenetic and sexually perfect females lay eggs. The adelgids were formerly called *chermes* but recent taxonomic study has shown that this name, by right of priority, belongs to certain of the jumping plant lice of the family Chermidae. Thus the name *chermes* must be replaced by the name *adelges,* in spite of the fact that these insects have become well known, not only to entomologists but also to foresters and others, by the former name. But the temporary confusion that is bound to result will not be so serious as the permanent confusion that would certainly occur if the common name *chermes* were retained for the adelgids.

The adelgids all feed upon coniferous trees and, in some instances, they are responsible for much injury. In general, they may be regarded as more injurious than the true aphids. They are particularly injurious to trees that are growing under unfavorable conditions. The life cycle of these insects is even more complicated than that of the true aphids. Most of the species have alternate hosts, but in every case the primary host is a spruce. On the spruce, the adelgids form leaf galls of different types, varying from a condition in which the bases of the needles are slightly swelled to a condition in which the needles of the new growth form a closed, cone-like gall. Where these galls are formed, a part or the whole of the infested portion dies. It would seem that when a large proportion of the tips are attacked, year after year, serious injury to the trees would result. Investigations by Wilford (1937) indicate that even heavy galling has little effect on the growth rate of trees infested with *Adelges abietis.* In the Northwest, however, adelgids have at times been responsible for serious injury, particularly to Sitka spruce.

The alternate or secondary host of the adelgids varies with different species (Fig. 140). It may be any one of the following genera: Abies, Pseudotsuga, Larix, Tsuga, or Pinus. On the secondary host no gall is formed. The insects live upon either the bark or the needles. The injury that they do to the secondary host may or may not be severe. In the case of the pine barklouse, *Pineus* (*Adelges*) *pinicorticis,* the injury is sometimes very severe. It is especially injurious to young trees growing under semisuppressed conditions and to older trees on poor sites. The activities of this insect may frequently so weaken

the trees that they succumb to the attack of bark beetles. The full life cycle of the pine bark-louse is not known. Another adelgid (MacAloney, 1935; Balch, 1936) that sometimes causes serious damage to the secondary host is the balsam wooly-aphid,

FIG. 140.—Adelgids on a secondary host, white pine. On this host the insect is called *Pineus* (*Adelges*) *pinicorticis*. (*University of Minnesota.*)

Adelges piceae. This is a European species that has been in this country for at least 30 years. Recently it has been especially injurious and has killed much balsam fir in the Northeast. Its numbers may be reduced by low temperature because −30°F. will kill all of these insects that are above the snow line.

The adelgids are small insects, oval in shape, with mouth parts of the sucking type. They are provided with wax glands that excrete a flocculent, waxy mass that covers the insects and

their eggs. Like the aphids, the adelgids have some winged generations and others that are wingless.

Adelges cooleyi is one of the American species that has been carefully studied. Its life cycle will serve well as an illustration of that of the group as a whole. This species may breed upon several primary hosts. It has been reported as attacking colorado blue-spruce, *Picea pungens;* engelmann spruce, *Picea engelmanni;* and sitka spruce, *Picea sitchensis.* The secondary host is douglas fir, *Pseudotsuga taxifolia.*

The species overwinters as an immature stem mother, or *fundatrix vera* as she is sometimes called. This stem mother is always found on spruce and always hatches from a fertilized egg. She is a wingless agamic female. When spring arrives, she soon completes her development; during this period she secretes a large quantity of white, waxy wool. When she becomes mature, she deposits a large number of unfertilized eggs beneath this wool-like covering. These eggs laid by the stem mother give rise to a generation called *gall dwellers* or *gallicolae.*

As soon as the young gall dwellers hatch, they make their way to the expanding new growth. There they settle down to feed. Each tiny individual takes up her position at the base of a young needle on an expanding tip, sometimes alone but often with some of her sisters. She inserts her mouth parts into the succulent tissues and sucks the sap. The stimulation resulting from the combined effect of the stem mother and her offspring the *gallicolae,* the exact nature of which is unknown, causes the basal portion of the leaf to thicken and expand, until it forms a shelter over the young insects. Usually all the needles on a shoot are attacked at practically the same time and respond in similar manner. These basal leaf swellings coalesce and form a cone-like gall on the new growth (Fig. 141). The form of the gall varies with different species of adelges but is constant for the same species. The individuals that arise from a single stem mother may number from 300 to 500. When the gall dwellers are full grown, the galls open. The young adelgids then crawl from the gall and settle on the spruce needles. Here they cast their nymphal skins and emerge as winged insects. This takes place about the middle of June.

These winged forms are called *gallicolae migrantes* or *migrating gall dwellers.* They fly to douglas fir and, after settling upon

the needles, each insect lays from 100 to 150 eggs. In some adelgids the winged generation of gall dwellers has two alternatives. They may either migrate to the secondary host or remain upon the primary host. In the latter case they are called *gallicolae non migrantes*, or *nonmigrating gall dwellers*, and give rise to forms similar to the true stem mothers, which overwinter and lay eggs, in the following spring, for another generation of

FIG. 141.—*Adelges cooleyi* galls on spruce. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

gallicollae on the primary host. In this way, a complete asexual cycle may occur on the spruce. *Adelges abietis* has this asexual cycle on the primary host without any migration to a secondary host.

The eggs on douglas fir laid by the *gallicolae migrantes* hatch in about 1 week into forms that are called the *colonist broods* or *colonici*. These are wingless forms that differ in appearance from the spruce-inhabiting forms from which they arose. The members of the *colonici* generation that arise from the *gallicolae migrantes* are sometimes called *false stem mothers* or *fundatrices spuriae*. They pass the winter on the secondary host in a

partly developed condition. Early in the following May they complete their development and deposit unfertilized eggs. The eggs in this generation are not so numerous as in those preceding. Each female lays from 30 to 60.

The young which hatch from these eggs are dimorphic in character. A part of them are wingless and remain on the douglas fir, while a part are winged and fly back to the primary host. The latter are called *sexuparae*. These that remain on the douglas fir form the spring brood of apterous females on the secondary host, which later lay unfertilized eggs. From these, the summer brood on the secondary host hatches. The members of the summer brood on the secondary host pass the winter in the immature form and, in their turn, become false stem mothers in the spring following. Thus on the douglas fir, there is a complete asexual cycle. This cycle on the secondary host, and that previously mentioned on the primary host, may continue indefinitely (Fig. 142).

FIG. 142.—*Adelges cooleyi* on the needles of douglar fir, a secondary host of this species. (*R. N. Chrystal.*)

The *sexuparae* fly back in early summer to the primary host and settle there. They give rise to still other forms, the true males and females. This stage has never been observed in America, but in England, Chrystal (1922) has found them, and doubtless they occur in this country. These sexual forms mate, and the females deposit a small number of fertilized eggs on the spruce. These produce the true stem mother or *fundatrix vera*.

Thus in adelges there occur three distinct cycles of development: the asexual cycle on the primary host, the asexual cycle on the secondary host, and the cycle on both the primary and secondary hosts, in which the sexual forms appear. Apparently, any one of these cycles may continue indefinitely.

No feasible method for controlling adelgids in existing forests has ever been suggested. It is possible that forests of the future

may be protected from adelgids by the selection of resistant tree varieties, as previously suggested. On shade and ornamental trees adelgids may be controlled by spraying. Because of their covering of woolly wax, these insects are difficult to kill with a spray. Chrystal has found that on the secondary host they are most susceptible in late winter when they are almost without this covering. This is also true of the young stem mothers on the primary host. On the primary host, sprays are obviously useless when the insects are within the gall.

Almost any strong contact insecticide is effective. Because of their waxy covering, sprays for these insects should be strongly soapy or should contain an oil. In England, the following formula for nicotine emulsion has been recommended: ¾ ounce of 90 per cent nicotine, ½ pound of soft soap, and 10 gallons of soft water. The following directions accompany the formula: "Dissolve ½ pound of soap in 4 pints of boiling water, allow the solution to cool and then add ¾ ounce of 90 per cent nicotine. Stir well and keep in a well-corked bottle. To use, take 1 (fluid) ounce of the concentrated solution and make up 1 pint with soft water." This gives a dilution of approximately one part of nicotine to 250 parts of water. Nicotine sulphate at this rate in a strong soap solution would probably give equally good results. Nicotine oleate, the formula of which was given under aphid control, should also give satisfactory control when applied in late winter or very early spring. Miscible oils should also prove satisfactory for sprays or dips. Gambrell (1934) recommends the use of a dormant lime-sulphur spray for this insect.

Adelgids on lawn trees may sometimes be effectively controlled by washing the trees thoroughly with a forcible stream of water from the garden hose. Pruning the galls, before they open, from small trees of the primary host may be desirable under certain conditions where other larger host trees are not near by. In forest plantations, the trees are particularly susceptible to injury by adelgids during the first few years after planting. For this reason, it is important that adelgid-free planting stock be used. Before being set out in plantations, all infested nursery stock should be dipped in one of the spraying solutions mentioned above or fumigated with hydrocyanic acid gas as previously described.

In the forest, certain biotic agencies are operating to bring about a natural control. Among these are certain parasites, predatory insects like the coccinellids, the syrphids, or the aphis lions, and predatory mites and spiders. Inasmuch as the most susceptible trees are those that are growing under unfavorable conditions, it is apparent that any improvement of growing conditions will reduce the danger of injury. Proper thinning, intelligent drainage, and careful selection of planting sites to suit each species, are some of the practices of good silviculture that will aid indirectly in controlling adelgids.

THE SCALE INSECTS

The scale insects, Coccidae, comprise another family of the Homoptera that includes many dangerous tree insects. Because they are so different in habits and appearance from the other Homoptera, and because of their great economic importance, they will be discussed here in a separate section. They are usually regarded as being particularly injurious to shade and orchard trees, although they are really equally dangerous in the forest. Their inconspicuousness, coupled with the fact that their work is often supplemented by that of other more conspicuous species, has resulted in a general underestimation of the importance of scales as forest pests. Recently, however, several severe outbreaks in forests have been reported. For instance, the black pine-leaf scale, *Aspidiotus pini*, has been responsible for heavy injury in parts of the Lake states and has also been injurious in California forests.

The scale insects are peculiar. No one on seeing these creatures for the first time would guess that they were insects. In fact, it is doubtful if on cursory examination a person unfamiliar with them would even regard them as living organisms. They are, for the most part, small to the point of minuteness and many of them appear as tiny scales of wax adhering to the leaves or bark. Others look like small galls, whereas still others appear to be accumulations of granular waxy material, or masses of resinous exudation upon the trees. Although this group includes many important pests, some very useful insects are also members of the family. For instance, the lac insects excrete over their bodies a resinous material which is an important article of commerce. This material, called *stick-lac*, is manufactured into

shellac. Before the days of coal-tar dyes the lac insects and other scales, like the cochineal insects, were important in the production of coloring materials.

The scale insects are numerous in species and variable in habit and appearance. Three groups of the family contain dangerous forest and shade-tree pests. These are the armored scales, the tortoise scales, and the mealybugs. The life history and habits characteristic of each group are quite different, and, therefore, a representative of each one will be discussed.

The Oyster-shell Scale.—One of the armored scales, the oyster-shell scale, *Lepidosaphes ulmi*, will be considered first. This insect belongs to the subfamily Diaspini, which is characterized by the scale-like covering beneath which the insect lies. This scale is composed in part of molted skins and in part of waxy or resinous excretions of the insect.

The oyster-shell scale is well known to almost everyone who works with woody plants. This insect attacks a great variety of fruit trees and deciduous forest trees and shrubs (Fig. 143). In the forest, the ashes, poplars, willows, and maples are probably the most susceptible trees. This insect is distributed throughout the temperate regions of the world and is either native to America or was introduced in very early colonial days, probably from Europe. It now occurs throughout temperate North America from the Atlantic to the Pacific.

The oyster-shell scale is well named. It has the general shape of an elongate oyster shell. The full-grown scale is about $\frac{1}{8}$ inch in length and brown in color. When these insects are abundant, the small branches of the infested trees may be almost completely encrusted with the scales. The male scales are said to be very rare. The exact proportion of males to females has never been determined, but it is so low that according to Griswold (1925) thousands of scales may be examined without finding a male. This suggests that this species usually is reproduced parthenogenetically, although no general acceptance of such an assumption is evidenced in published writings on this insect.

In the North, the eggs are deposited in late summer or early autumn and pass through the winter without hatching. In the early spring they hatch. The time of hatching varies greatly, depending upon the latitude and the season. In general, it corresponds in time to the dropping of the apple blossoms. The

young insects creep from beneath the mother scales, by the hundred, and wander about on the bark of the host tree. At this time they may creep upon birds, other insects, or anything else that comes in contact with the trees. In this way, they may be carried from tree to tree, or even from locality to locality.

FIG. 143.—A branch of aspen almost completely covered by oyster-shell scales, *Lepidosaphes ulmi*.

After wandering aimlessly about over the bark for some time, the young settle down in a suitable place, insert their mouth parts, and proceed to feed upon the sap of the tree on which they are resting. The secretion of the scale then begins. The female scales never move again but live for the remainder of their life beneath the scale. As the insect grows, the scale is increased in size so that the body is always entirely covered. When mature, the female has lost both legs and eyes. She is little

more than a reproductive sack with sucking mouth parts through which the food is drawn. The male, on the other hand, undergoes an entirely different type of metamorphosis, and, after passing through a stage resembling the pupal stage of holometabolous forms, he emerges in the form of a tiny insect with antennae, compound eyes, two wings, and the mouth parts replaced by

FIG. 144.—The scurfy scale, *Chionaspis furfura*. (*University of Minnesota.*)

a second pair of rudimentary eyes. The male takes no food and is short lived.

By the time the female is full grown, her body is filled with eggs. As she lays them her body shrinks in size, until almost the entire cavity beneath the scale is occupied by eggs and, in consequence, the mother is crowded into a small portion of the anterior part. Shortly after oviposition, the female dies; consequently, by late autumn there are no females alive. The number of eggs deposited by each female varies from 20 to slightly more than 100. In the North, there is only one generation of this insect each year. In the South, there are two genera-

tions. Where there are two generations, the eggs of the first brood are deposited early and hatch during the month of July.

Other important species of armored scales pass through life cycles very similar to that of the oyster-shell scale. The scurfy scale, *Chionaspis furfura* (Fig. 144), and the pine-leaf scale *Chionaspis pinifoliae* (Fig. 34), both pass the winter in the egg stage and develop in a manner quite comparable to that of the oyster-shell scale. Other members of this group pass the winter in a partly grown condition and complete their development in the following spring. In some of these scales the eggs hatch within the body of the female, and the young are born alive.

The control of scale insects is very much the same for all species. Instead of taking up the question of control in each individual case, scale control in general will be discussed at the end of this section.

The Cottony Maple-scale.—The tortoise-scale group is well illustrated by the maple scale, *Pulvinaria vitis*. This group of scales is so called because of their tortoise-like form. Some members of this group secrete very little wax and are, therefore, called *naked scales;* others, like the cottony maple-scale, are naked but excrete wax to form an egg sack; whereas still others excrete wax in abundance. Unlike the armored scales, the legs of many tortoise scales are not reduced to the point of uselessness, at least not until the female becomes filled with eggs. They may, therefore, change their location when partly grown. The scales of this group are, for the most part, much larger and more conspicuous than the armored scales. Many of them excrete large quantities of honeydew, which may coat over the leaves and branches of infested trees. A black fungus that grows in the honeydew, usually gives the infested trees a decidedly black appearance, which is often very unsightly.

The cottony maple-scale attacks maples, particularly the soft maple, throughout the range of its host trees and, when abundant, may kill trees. Previous to cold weather, the female is fertilized, and she spends the winter in a partly developed stage on the small branches of the host. With the arrival of spring, these females complete their growth. When full grown, they are large for scale insects, sometimes being considerably over $\frac{1}{8}$ inch in length and broadly ovate in form. Their color is a dark brown. Full growth is attained early in the summer, at which

time they begin to lay their eggs. The specific name *innumerabilis*, which has sometimes been applied to this species, describes well the fecundity of this insect. A comparatively unproductive individual will lay 500 eggs, while some females may produce several thousand. The biotic potential of such a species is

FIG. 145.—The cottony maple-scale, *Pulvinaria vitis*, on soft maple. (*University of Minnesota.*)

tremendous. If the factors of environmental resistance were reduced, it is obvious that, with such a high potential, this insect would multiply at an almost unbelievable rate.

The high fecundity of this species may be remarkable, but it is not the only interesting fact in connection with its reproduction. As in the case of some other members of the tortoise-scale group, the eggs are laid in egg sacks constructed of cotton-like wax. A conspicuous, white, cottony mass that is filled with eggs is

extruded from beneath the caudal end of each mother scale (Fig. 145). These white masses stand out prominently against the blackened bark of the trees and naturally attract much attention. Some other species of the tortoise-scale group, instead of depositing their eggs in egg sacks as does this species, lay them beneath their arched bodies; whereas still others produce living young.

The tiny young scales leave the egg sacks in July or August and make their way to the leaves. There they settle down and feed until fall. Most of them locate on the lower side of the leaves along the large veins. The males develop much more rapidly than the females and emerge as winged adults in late summer or fall. At that time mating takes place even though the females are not fully developed. After fertilization and before the leaves fall in the autumn, the females migrate from the leaves and make their way back to the twigs and small branches where they pass the winter, complete their development, lay their eggs, and die.

The European Elm-scale.—The European elm-scale, *Gossyparia spuria*, is a member of another group of scale insects, the mealybugs. The members of this group are best known as pests of greenhouse plants, but some of them are injurious to trees, particularly in the South. Even in the North, however, some of our most injurious scale insects belong to this subfamily. The mealybugs excrete a powdery wax, which covers their bodies. This flour-like excretion gives them their common name.

The European elm-scale is one of the most dangerous tree pests of all the mealbybugs. This insect is one of our foreign guests which we could well do without. It was first discovered in this country in New York State in 1884, but it had apparently been established for some time previous to that date. In 1894 it was reported from California, and it is now known to be widely distributed throughout the United States and Canada. Wherever it makes its way, it becomes a troublesome and dangerous pest of elms. So far, it has not become a forest pest, and for the most part it is confined to shade trees in cities and towns.

When this pest first appears in a locality, it is usually very injurious. It attacks all species of elm and becomes abundant. Heavily infested trees are likely to succumb. If the trees are not killed in the early years of the outbreak, however, they are likely to survive. Perhaps the trees are able to build up a resistance to the pest, or perhaps the scale is brought under control by its

natural enemies. This will probably be the history of the insect if it gets into a forest. Natural enemies will control it. But while a new biotic balance is being attained, much injury may be expected to result.

The chief way in which new infestations may occur is by transporting the pest to new localities upon infested nursery

FIG. 146.—A mass of female, European elm-scales in the third stage. Note the semicocoon surrounding each insect. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

stock. The overwintering scales may easily be carried from place to place in this way. The other means of dispersal (on wind-blown leaves, on birds or insects, by ants, or by the scales creeping from tree to tree) are slow and account only for local, gradual spread.

The body of the European elm-scale is ovate in form. In the second stage this species excretes a powdery wax like the other mealybugs. The third-stage females are brown in color and without any dorsal covering. They do, however, excrete a

white waxy fringe which curves upward from the ventral side and partly encloses the body (Fig. 146). This is called the semicocoon. The males, between the second stage and the adult, are enclosed in white, waxy cocoons.

The life cycle of this insect is similar, in many ways, to that of the other scales discussed. The winter is passed on the branches of host trees in the second instar. Their covering of powdery wax serves to protect them to some degree against both excessive desiccation and excessive moisture. Very early in the spring, or even in late winter, the males molt to the third stage and spin their waxy cocoons. After completing their coccons, they molt again. This fourth stage, the prepupal, is a quiescent stage within the cocoon. In the course of a week or more the prepupa molts again. It is then a pupa. After another quiescent period the adult males emerge from the cocoon. The first males to emerge are wingless; the later emergents are winged. Between these two extremes are insects with all stages of wing development.

In the meantime the females have also been undergoing a certain change. About the time that the adult males are ready to emerge from their cocoons, the females molt for the last time. The males emerge and mating takes place. The fertilized females then seek out a suitable location, usually on the underside of a branch, and settle down for the last time. They then begin to excrete the conspicuous fringe of white wax, the semicocoon, that partly envelops the body. During this third period of her life the female excretes large quantities of honeydew, which drops onto the branches and later onto the foliage and upon the ground beneath the trees and covers everything within range with a sticky coating. In this sweet material a black fungus grows, and soon the infested trees assume an inky-black appearance.

By late spring, the females are fully grown and have completed their semicocoons. They are then ready to lay their eggs. The egg-laying period of most insects is brief, but this insect takes her time in performing this important process. Oviposition may last for several months. The eggs are held in the body of the mother until they are about ready to hatch at which time they are expelled. The vulva opens ventrally so that the eggs are deposited beneath the mother's body where they are protected until hatching has been accomplished. Each female lays a large

number of eggs, although by no means as many as does the cottony maple-scale.

In less than an hour after the eggs are laid the nymphs hatch and leave the mother. They migrate to the leaves where they settle down to feed. During this stage little wax is excreted, and, except for the pubescence of the leaves, they are without protection. Some 6 weeks after hatching, they molt for the first time. In this stage a powdery wax covers the body. With the approach of autumn, most of the young scales move from the leaves and locate themselves upon the branches and trunk. Those that fail to do this drop with the leaves and most of them probably starve. Some are said to creep up the trunks of convenient trees, where they establish themselves. Thus the insect may be spread from tree to tree on wind-blown leaves.

Control of Scale Insects.—Scale insects are very difficult to control even on shade and nursery trees. For that reason, it is particularly important that every possible precaution be taken to prevent the introduction of scales into uninfested localities. Planting stock should be carefully inspected, and if scale infestation is found the stock should be rejected, because no treatment of infested stock will give perfect results.

When once infested with scales, a forest will always remain infested and only by means of natural factors can these pests be held in check. Fortunately, there are many valuable agencies of natural control. Unfavorable weather conditions, for example, heavy washing rains during the migration of the young scales, may reduce the numbers of the insects materially. In 1925, heavy rains during June checked a dangerous infestation of the black pine-leaf scale, *Aspidiotus pini*, in the jack-pine region of Minnesota.

Like most other insects, competition among themselves appears to be a control factor, in some cases. When the suitable parts of a tree become heavily encrusted with scales, the fecundity of the individual is apparently much reduced, because of food shortage. In still more severe cases, the death of leaves or twigs upon which the scales are feeding may bring about an acute food shortage and ultimate starvation for many scales.

Predaceous insects, like the ladybird beetles, feed upon scales. The adults and the larvae of these beetles both participate in this valuable work. The larvae of the lacewing flies, Chrysopidae,

are also important enemies of scales. Among the most important of the predatory groups that feed upon scales are the mites. All mites that are observed under or near scales are not necessarily predaceous. Some of them are scavengers but many of them, like *Hemisarcoptes malus*, are important predatory forms. This particular species feeds upon the oyster-shell and San José scales and is very important in controlling these pests. Tothill (1918) reports that this is by far the most important agency of control of the oyster-shell scale in eastern Canada (Fig. 164).

Certain small hymenopterous parasites are also important in keeping scale insects in check. *Aphelinus mutilaspidis* is one of the important parasites of the oyster-shell scale.

In some cases, it has been possible to regulate the activities of some of these biotic factors of control, and thus use them directly against a specific pest. For instance *Rodolia* (*Vedalia*) *cardinalis*, a coccinellid, has been introduced into California to control the cottony cushion-scale, *Icerya purchasi*, and has proved very effective. The beetles have been reared and liberated where they were most needed. Tothill suggests that Hemisarcoptes might be handled in a similar manner to control the oyster-shell scale. But as we have seen in a previous chapter, we are not yet able to make full use of these biotic factors of environmental resistance in direct control work.

Chemical methods of direct control must be resorted to. Spraying and fumigating are the two most important means of coccid control that are at our disposal. These methods are not of course, applicable in the forest, but they can be used to advantage on nursery stock. Fumigation of nursery stock with hydrocyanic acid gas is, perhaps, the best method available for treating scale-infested materials. If properly done, this treatment will give good control for practically all scales.

Spraying of shade and other ornamental trees with a contact insecticide gives reasonably good control, but in most instances repeated applications are necessary. The small armored scales are susceptible to lime sulphur at the rate of 1 part to 9 parts of water. This material should be applied in the spring just as the trees are beginning the season's activity. This material has not proved satisfactory for the oyster-shell scale and some other closely related forms. Neither is it effective upon large scales like the cottony maple-scale and the European elm-scale. For

these scales a dormant spray of a miscible oil is generally used. Spraying with nicotine extract at the rate of 1 part of nicotine to 500 parts of soapy water will kill all the different species of young scales. Such a spray repeated once a week, during the hatching period, is an excellent method of control.

A simple method that has proved satisfactory in the control of some of the large scales, like the cottony maple-scale and the European elm-scale, is to wash the trees with a hard stream of water. On small trees, this can be accomplished by use of the garden hose. On larger trees, a larger hose and higher pressure are necessary. On the whole, however, this is not so satisfactory a method as spraying with miscible oil.

CHAPTER XVI

INSECTIVOROUS PARASITES

The part that parasites and predators play in environmental resistance has already been seen in Chap. IV, and in Chaps. VI and IX is explained how they may be used either directly or indirectly in the control of insect pests. Furthermore, it has been seen that parasites and predators are to be found in many groups in the animal kingdom. In this chapter, a few representatives of some of these groups will be discussed.

ENTOMOGENOUS MICROORGANISMS

Certain members of each of the different groups of microorganisms attack insects. Some of the types of insect diseases caused by them are bacterial diseases, fungous diseases, and protozoan diseases. It is generally believed that the filterable-virus diseases are also caused by microorganisms, but these organisms have never been isolated in connection with any filterable-virus disease. The part played by some of these organisms in parasitizing insects will now be considered. Examples of bacterial, fungous, and the polyhedral type of filterable-virus diseases will be cited as illustrations. Because so little is known concerning the part played by protozoan diseases in connection with insect activities, no examples of these will be discussed.

Bacterial Diseases.—References to bacterial diseases of insects are exceedingly common in entomological literature. In many instances, the diseases mentioned were undoubtedly caused by bacteria, but, owing to the difficulties attendant upon the conclusive identification of the causative organisms and to the general unfamiliarity of entomologists with bacteriological technique, many incorrect determinations have resulted.

Epidemics of bacterial insect diseases usually occur only when the host is extremely abundant. This is probably because they are, for the most part, infectious in character, and it is only when

the population of the host is quite dense, with the resultant frequent contact between the individual insects, that conditions for infection are at their best. Some of the most serious bacterial diseases of insects gain entrance into the digestive tract along with the food. There they multiply and attack the host tissues. The method of entrance in many instances is unknown. These disease organisms may attack insects in any stage, but those that we now consider as being most important are the cause of larval diseases.

The symptoms of the diseases vary somewhat. As a rule, however, the first symptom appears to be a loss of appetite on the part of the affected larvae. Later, these larvae cease to eat and finally die. Previous to and following death, changes in color usually occur. Often this color change is first indicated by a fading and yellowing of the natural larval colors. Later, usually after death, the larvae become much darkened. After death has occurred, a rapid disintegration of the internal tissues takes place until finally the skin is filled with a dark liquified material. Frequently, the insects suffering from one of these parasitic diseases will continue to hang to the plant on which they were feeding, even after death.

Outbreaks of bacterial diseases are frequently correlated with weather conditions. Cool, moist weather followed by a warm period is, in most cases, conducive to epidemics. This suggests the probability that cool, moist weather is favorable for infection, and that warm weather is conducive to the rapid growth of the organism. Perhaps, under comparatively cool conditions, the growth of the bacteria may be sufficiently slow to permit the continued development of the infected larvae, but this is only conjecture.

In 1915 an interesting and perhaps valuable bacterial parasite of the gypsy moth was unintentionally shipped into this country from Japan. Glaser (1918) described the symptoms and characteristics of the disease caused by this bacterium and determined, to his own satisfaction, that it was not previously present in America. This organism, described as *Streptococcus disparis*, will serve well as an illustration of a bacterial parasite.

This is one of the parasites that gains entrance into the body of its host, along with ingested food. The parasite lives and multiplies in the insect's intestinal tract. The first effect upon

infected larvae is to produce a violent form of diarrhea accompanied by loss of appetite. In the early stages of the disease, the organism is confined to the alimentary canal, but as the disease progresses the muscle tissues also become involved. Finally the affected larvae cease to eat, lose all muscular coordination, and die. After death they usually continue to hang by their prolegs. Then the tissues rapidly disintegrate. During the early stages of the disease the larvae contaminate the foliage on which they are living, thus passing on the parasite to other larvae that eat the contaminated leaves. In this way the disease spreads rapidly, especially when the gypsy-moth larvae are numerous.

Fungous Diseases.—Entomogenous fungi are not at all uncommon among insects and sometimes, as in the case of the chinch-bug disease mentioned in Chap. VI, may be largely responsible for checking an outbreak. As we have previously pointed out, the direct use of these organisms in control is made very difficult, because their effectiveness depends upon certain favorable weather conditions.

Most of the studies of these fungi that have been made have not been concerned with forest insects. Hewitt (1912), however, in connection with his study of the larch sawfly, has investigated one of them. He found that this fungus, *Isaria farinosa*, in some localities both in England and Canada, was responsible for the death of a very large percentage of the cocooned larvae. Hewitt has shown that the larvae become infected after dropping from the trees in search of suitable hibernating quarters. The Isaria fungus lives, as does a saprophyte, on the moss beneath the trees and its spores are capable of infecting larvae that crawl over the infected moss. The effectiveness of the disease depends upon the abundance of saprophytic growth, which in turn depends largely upon moisture conditions (Fig. 147). After having been infected by the fungus, the larvae proceed normally to spin their cocoons, after which they succumb to the disease. The external appearance of the larvae changes. They lose their greenish color and by the time of death, become pinkish white. Finally, the larvae are completely mummified within the cocoon.

The growth of this fungus within the body of the host was not studied by Hewitt, and hence we do not know exactly what the internal effects were. It is probable, however, that they may

be similar to the effects of other closely related diseases. In some of these, yeast-like bodies appear in the blood a few days after infection (Speare, 1920). These cells multiply rapidly, increasing in number until the blood takes on a milky appearance. Finally, the blood becomes so filled with these *blastocysts*, as they are called, that circulation ceases and the larvae finally die. When the blood ceases to circulate, the blastocysts, although they continue to form, do not break off from the parent cell, with the result that colonies of individuals are formed that later become resting spore masses. The saprophytic growth on the moss, mentioned above, presumably arises from these spores. When the nutriment in the blood is exhausted, other tissues are attacked until all the organs are destroyed.

FIG. 147.—A larch-sawfly cocoon on which is growing the entomogenous fungus, *Isaria farinosa*.

There is some difference of opinion concerning the manner in which entomogenous fungi grow within the insect body. Some authorities claim that the growth resembles branching hyphae. Speare (1920) maintains that, although this may be true in some diseases, it is not the case with the species of Isaria, Sorosporella, and Botrytis that he has studied. These organisms, he states, multiply by the division of yeast-like cells as described above. Furthermore, he points out that this method of multiplication "seems especially well adapted for reproduction in a liquid menstruum such as insect blood, the circulation of which carries them to all parts of the body cavity and continually supplies them with fresh nutriment."

Polyhedral Diseases.—The consideration of an exceedingly interesting group of insect diseases that, judging by their reactions, are supposedly caused by organisms will now be taken up. The organisms, however, have never been isolated. These diseases of insects are very similar to some of the most dreaded diseases of man and other mammals; hydrophobia, smallpox, and trachoma, for instance. They are characterized by the presence of granular bodies in the blood and in certain tissues. In insects, these bodies are called *polyhedra*. The nature of these polyhedral bodies has long been a point of controversy; some maintain that they are chemical by-products of the disease

organisms, whereas others claim that they represent a stage in the life cycle of the disease organism. Which of these opposing views is correct has not yet been settled, but experiments have proved that the virus of the polyhedral diseases is capable of passing through Berkfeld *N* candles, through which the granular polyhedral bodies fail to pass.

Although their true nature is not known, these diseases are among the most effective parasites in the natural checking of outbreaks of certain lepidopterous insects. Up to the present time, the polyhedral diseases have never been found attacking insects other than representatives of the Lepidoptera. Among the most important of these diseases, in America, is the wilt disease of the gypsy moth and the wilt of the tent caterpillar. It is possible that these may not be two distinct diseases, but up to the present they have been so regarded.

The gypsy-moth wilt is apparently identical with the *Wipfelkrankheit* of the European nun-moth and was not present in America previous to 1900 (Glaser, 1915). Presumably it was accidentally introduced into this country long after the gypsy moth became firmly established. Now it is distributed throughout the infested region where it is of material aid in keeping the pest in check.

Like the bacterial diseases, the wilt disease is infectious. It gains entrance into the body of the insect through the mouth with ingested food. After becoming established within the insect, it attacks and kills the blood cells and certain other tissues, with the result that the caterpillar usually succumbs. In certain instances, however, the insect is able to survive, complete its development, emerge as a moth, and reproduce itself without showing any external indications of the presence of the disease. In such instances, the infection may be passed on through the egg to the progeny. Because of the presence of these chronic carriers, one can never be sure that the disease is not present, even though the caterpillars in a locality may appear to be healthy. Under high-temperature conditions, these chronic cases may become acute, with the result that the host will be killed and an epidemic will be started among the larvae.

Epidemics of wilt have been especially common whenever the gypsy moth has become very abundant and stripped most of the

foliage from the trees on which they were feeding. Under such conditions, the larvae are exposed to much higher temperatures than normal, because the direct rays of sun can shine through the crowns of the trees upon them. When once the disease breaks out, the mortality is exceedingly great. Sometimes it amounts almost to extinction. In Europe, the outbreaks of this disease among the nun-moth caterpillars have, likewise, frequently resulted in the almost complete extinction of the host.

The larvae, when infected with the wilt disease, first become sluggish and then stop eating. Before dying they have a tendency to climb high up in the trees and, after death, they remain there hanging by their prolegs. The tissues of the body become darkened, decomposed, and liquefied. The larvae hang flaccid until finally they have completely disintegrated, and they then dry upon the tree. These dried smears that were once larvae remain infectious for a long time, and it is thought probable that plants on which nun- or gypsy-moth larvae had died may have been shipped from Europe into this country, thus bringing about the inoculation of the gypsy moth in America.

PARASITIC INSECTS

Of all the groups of parasites that attack insects, the parasitic insects have received most attention from entomologists. Parasitic insects do not constitute a phylogenetic unit but are to be found in many different orders of insects and in widely divergent families within these orders. The great majority of the most valuable species belong either to the Hymenoptera or the Diptera.

General Characteristics.—The adult stages of parasitic insects vary greatly in form, but the larval stages are very similar in appearance. The larvae are practically all legless grubs, maggot-like in form. Most of them are able to move about only with difficulty. The mouth parts, except in the early stages, are much reduced or in some instances they may be vestigial. Thus, they are specialized for a mode of life which is characterized by an abundance of easily obtainable food, and they illustrate the condition that is called *specialization by reduction of parts.*

The adults, on the other hand, are specialized to insure successful infestation of the host. This is accomplished in a number of different ways by the parasites belonging to the various groups.

The Sarcophagidae and some of the Tachinidae are larviparous. This adaptation, by eliminating the helpless egg stage, increases the probability of successful entrance of the parasite into the host. Many Tachinidae that are not larviparous stick their eggs firmly to the body of the host, whereas others attach them to the substratum on which the host is found. Most of the Ichneumonoidea are provided with an elongate ovipositor which they thrust either into the host or into its cocoon, and there deposit their eggs. Others of this same group are said to place their eggs in the galleries of wood borers, and the larvae when they hatch creep along the gallery until they find the host. *Megarhyssa* (*Thalessa*) *lunator* (Fig. 29), which is one of the largest of the Ichneumonidae and a parasite upon the pigeon tremex, *Tremex columba*, is said to have this habit. But in view of the fact that the borers of the family Siricidae, of which the pigeon tremex is a member, pack their burrows full of frass as they progress, the eggs of the parasite must be placed very near the host, if not actually on its body. The large ichneumonids are remarkable for the fact that they are able to drill through solid wood, in order to place their eggs in a favorable position in or near their host. The Chalcidoidea are smaller than most of the ichneumonids and usually deposit their eggs within the body of their host, although some species of this group, as well as some of the other Hymenoptera, are able to feed externally. In the case of external feeders, the host usually dies soon after it is attacked, or, in some instances, it is killed by the adult parasite at the time of oviposition (Graham, 1918). The Proctotrupoidea are mostly small hymenopterous parasites. Many of these tiny insects parasitize eggs, whereas others are larval parasites. As a rule, if they are larval parasites, they attack only small insects.

Parasitic insects are sometimes limited to a single host. These are called *obligate* or *specific parasites*. Others are able to attack a number of closely related species, whereas still others are general parasites, because they are able to attack and parasitize a great many different species.

Insects that are parasitic upon other insects are often regarded as being always beneficial to man's interests, inasmuch as they reduce the number of injurious species. Such a generalization is not entirely safe, however, for there are parasites that attack

either predaceous insects or insects useful to man in other ways. Thus, some insect parasites may be injurious. These species that attack and parasitize other parasites are called *secondary* or *hyperparasites* (Fig. 148). Hyperparasitism is known to occur to the third, fourth, and, possibly, fifth degree. This force

FIG. 148.—A hyperparasite, *Dibrachys boucheanus*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

reduces the effectiveness of parasites in holding down insect numbers and adds to the complexity of the part played by parasites in environmental resistance (Fig. 149).

The order Hymenoptera contains more species of parasites than any other insect order. In fact, three superfamilies are made up almost entirely of parasites and are often given the group name, parasitic Hymenoptera. These three superfamilies are the Ichneumonoidea, the Chalcidoidea, and the Proctotrupoidea. A representative from each of the first two of these groups will be discussed. Next to the Hymenoptera in number of parasite species comes the Diptera. One important representative of this order will be discussed.

The Ichneumonoids.—One of the ichneumonoids about which much has been written in recent years is *Apanteles melanoscelus*, an introduced brachonid parasite of the gypsy moth in New

England (Fig. 150). This is a small black insect, about 3 millimeters in length. It was introduced into this country from Europe, where it is one of the most effective of the natural enemies of the gypsy moth.

This insect possesses many characteristics that, from the viewpoint of man, are desirable in a parasite. Its biotic potential is exceedingly high. Crossman (1922) states that it is safe to assume that each female is capable of depositing in the neighborhood of 1,000 eggs. Although no data are given concerning the sex ratio, he infers that the sexes are approximately evenly divided or that perhaps there may be an excess of females over males. Inasmuch as this species is not polyembryonic, the biotic potential would be in the neighborhood of 500 for each generation. The life history of Apanteles is perfectly synchronized with that of the gypsy moth. It is active and persistent in its attempts to place an egg in its host and, under laboratory conditions, it will parasitize one larva after another for periods of from 30 minutes to 1 hour, as rapidly as they can be presented.

FIG. 149.—A parasite attacking a predator. The larva of an ichneumon parasite attached to a spider. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

Still another advantage that this parasite possesses is its ability to parasitize a number of small hairy caterpillars. In Europe, it is reported as a parasite of only the gypsy moth and the satin moth. In America, however, it attacks the tent caterpillar and several tussock moths, as well as the gypsy moth and the satin moth. This ability to transfer its activities to other species makes it possible for thsi parasite to maintain itself in spite of the periodical scarcity of gypsy-moth larvae.

Unfortunately, however, this insect suffers greatly from the attack of secondary parasites and ants, especially while it is in the overwintering stage. These reduce its numbers materially, thus preventing it from being as effective in checking the gypsy moth as it might otherwise be. Crossman (1922) reports a maximum

of 10 per cent secondary parasitism in the first generation and 75 per cent for the second or overwintering generation. But in spite of this high percentage of loss, a simple calculation will indicate that factors of environmental resistance, other than secondary parasites, are operating against Apanteles and are playing an important part in reducing the numbers of this para-

FIG. 150.—Adult and larva of *Apanteles melanoscelus.* (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

site. Otherwise, with its high potential, it would be able to overtake and exterminate its host in a very few years after becoming established in a locality, in spite of its secondary parasites. One of these resistance factors is, undoubtedly, the untimely death of many hosts, from other causes, before the parasites within them have reached full growth; for, obviously, when the host dies the parasite within it must die also. Furthermore, it must be remembered that parasites are density-dependent and become less effective as the host numbers are reduced.

The life history of *Apanteles melanoscelus* is similar in all but a few respects to that of other ichneumonoids (Crossman, 1922). Perhaps the most unusual feature is the fact that two generations of the parasite occur during the larval period of the host. Adults of the first generation emerge from their overwintering cocoons at about the time the gypsy-moth eggs are hatching. In the average season, this begins about the middle of May. This emergence extends over a period of about 3 weeks. The female parasites are able to begin oviposition very soon after they emerge.

Fig. 151.—Cocoons of *Apanteles melanoscelus*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

The act of oviposition requires only a second. The parasite comes up to a host larva, quickly inserts her ovipositor, lays a single egg, and withdraws her ovipositor in an almost unbelievably short space of time. Sometimes the caterpillar may struggle about and even may fall from the tree in its attempts to avoid the attacking parasite, but, according to Crossman, on whose statements this account is based, these attempts at evasion are usually futile.

In from 48 to 72 hours the eggs hatch, and the larvae make their way to the dorsal part of the posterior end of the body cavity. Here they usually remain until they are ready to emerge. They feed upon the fat cells and lymph of the host until they have passed through two instars. The third instar larvae of this first generation leave the host in from 7 to 13 days after the time they were inserted as eggs—a rather short period of development even for an insect.

The emerging larvae spin their pale yellowish cocoons near the place at which they emerge and there transform to the pupal stage (Fig. 151). A period of from 5 to 9 days is required before the adults emerge. Thus, the entire first generation

cycle may only require 14 days, although some individuals may require as long as 25 days.

In the meantime, most of the gypsy-moth larvae that escaped parasitization, or other mishaps, have only reached the third instar and still are sufficiently small in size to provide suitable

FIG. 152.—Cocoons of *Coeloides sp.* in galleries of *Ips oregoni.* (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

host material for the second generation of Apanteles. The few, however, which have passed beyond the third instar are fortunate, for their larger size and longer hair will make them much less susceptible to attack than are their smaller brothers.

Oviposition begins soon after the adult parasites emerge. The larvae of the second generation develop more deliberately than

those of the first. They require from 13 to 21 days to reach the third instar or almost twice as long as the time required in the first generation. The third instar larvae of the second generation spin cocoons that differ somewhat from those of the first generation. They are a trifle heavier and are a sulphur yellow in color. Within these cocoons the larvae pass the winter. The following spring, about the time the first gypsy-moth eggs hatch, these overwintering larvae, if they have survived the attacks of their enemies, transform to the pupal stage and, shortly thereafter, emerge as adults ready to start another spring generation of parasites.

Fig. 153.

The Chalcidoids.—The superfamily Chalcidoidea of the Hymenoptera contains a tremendously large number of species which differ more or less from one another in habit. Some of them are external or *ectoparasites* (Figs. 153, 154), whereas others live within the host and are called *endoparasites*. Some of them have a number of generations during a season, whereas others may have only one or

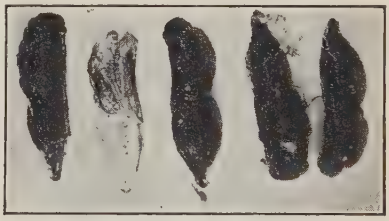


Fig. 154.

Fig. 153.—The larvae of *Eurytoma pissodis*, an ectoparasite of the white-pine weevil.

Fig. 154.—Pupae of the chalcid, *Eurytoma pissodis*.

two. Some are confined to a single host. Others are general parasites. They are all rather small in size and are usually black or iridescent in color.

The complete life histories of very few American species attacking forest insects have been studied in detail. One species, however, was studied by Hewitt (1912) which will serve well as an illustration of the chalcidoid group. This happens to be one of the Pteromelidae, *Coelopisthia nematicida*, and is an external parasite of the prepupal stage of the larch sawfly. Hewitt

considered it to be one of the most effective of the larch-sawfly parasites, but more recently another appears to be doing much more effective work (Watson, 1931).

Coelopisthia nematicida is known to be distributed throughout the eastern part of the United States and Canada wherever the larch sawfly occurs, and in all probability it is to be found throughout the entire range of the sawfly in America.

The winter is passed in the larval stage within the cocoon of the sawfly. The adults emerge in May or early June while many of the sawflies are still in the prepupal stage. These adults are very small, black insects about 2 millimeters in length. They immediately seek out cocoons containing healthy prepupae and deposit their eggs (Fig. 155). The oviposition of this insect is very different from that of Apanteles. The female, with deliberation, thrusts her ovipositor through the cocoon that contains her victim, and there she remains almost motionless for a long time. Hewitt observed one female which remained with her ovipositor inserted into the cocoon for a period of 1½ hours, and later, after a rest of 20 minutes, again inserted her ovipositor, this time remaining in the oviposition position for almost an hour. The eggs hatch in about 3 days.

FIG. 155.—*Coelopisthia nematicida*, a chalcidoid parasite of the larch sawfly, laying her eggs in a sawfly cocoon. (*Entomological Branch, Can. Dept. Agr.*)

The larvae of this parasite, like the adults, are very small, and as a result it is possible for a number of them to develop on a single sawfly prepupa. It is not at all uncommon to find from 50 to 75 of these parasites feeding within a single sawfly cocoon. It is probable that a single female may lay her entire quota of eggs in one or two cocoons, although we cannot be sure, for no data are available on this point.

The parasitized prepupa appears to be stupefied or dead even before the parasite eggs have hatched. Later on, after the larval parasites have begun feeding upon the blood and tissues, the host is obviously dead. Before the parasite larvae have fully developed, the host is almost entirely decomposed. This condition is very similar to that observed in the bee-moth larvae parasitized by a closely related pteromelid (Graham, 1918). In that instance the host larvae were killed by the parasite at the time of oviposition.

The larval stage requires about 12 days for its completion. When fully developed, they transform to the pupal stage within the cocoon of the host and later to the adult stage. The adults cut their way through the cocoon and emerge to seek new hosts. About 23 days are required for development under ideal conditions. This period is probably considerably lengthened under the cool conditions that exist in the tamarack swamps. On the basis of laboratory experiments, Hewitt concludes that six broods may be developed during a season. This may be possible under specially favorable conditions, but it is doubtful if this many generations occur in nature.

On first thought, it would appear that an insect of this sort, with a series of short generations, would be limited in its effectiveness as a parasite by the unavailability of suitable host material at certain seasons. Although this is true to a certain degree, it is not such an important limiting factor as might be expected. This is because sawfly prepupae are available at practically any time during the growing season. The period of greatest scarcity is during June, but even at that time many that have been delayed in emergence can be found. Thus, the parasites can obtain suitable host material at almost any season.

The Tachinids.—Among the parasitic Diptera, the various species of the family Tachinidae are probably the most valuable destroyers of forest pests. Like other groups of parasites, however, they are not all beneficial, for some parasitize beneficial insects (Collins and Hood, 1920). The habits of the tachinid parasites vary considerably. Some of them are oviparous, whereas others are larviparous. The oviparous species usually glue their eggs tightly to the body of the host to prevent their being rubbed off before they hatch. The larvae in those species that are larviparous are either deposited on the body of the host or are inserted by means of the larvipositor within the host's body.

One of the imported tachinid parasites of the gypsy moth that have become firmly established in America is *Compsilura concinnata*. It attacks not only the gypsy moth but also the browntail moth, the fall webworm, the white-marked tussock-moth, the forest tent-caterpillar, and many other native insects (Fig. 156). In fact, if it were not for its ability to adopt these new hosts when introduced into this country, it could not have become established here. Since its establishment it is said to have

exercised a decided controlling influence upon some of our native pests as well as upon the foreign gypsy and brown-tail moths (Culver, 1919). It has also played an important part in the control of a more recently introduced European pest, the satin moth.

Compsilura is widely distributed throughout the parts of Europe where the brown-tail moth is found. It has been introduced into America from no less than 10 different European countries and possibly from Japan. From this we are justified in

FIG. 156.—The adult of *Compsilura concinnata*, an imported tachinid parasite of the gypsy and brown-tail moths. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

assuming that it is a fairly common parasite in its native lands. It is a rather large, robust, hairy fly about 7 millimeters in length. Its coloring is a combination of black and white which gives the insect a gray appearance.

Compsilura is one of those larviparous tachinids that place their larvae within the body of the host. In parasitizing its host the adult female darts quickly at a near-by caterpillar, pierces the skin with a strongly chitinized piercing organ, inserts its larvipositor, and deposits a larva before the host insect can escape. The larvae, according to Culver, are usually inserted into the intestine; later they attach themselves, by means of anal hooks,

to some part of the tracheal system, often near a spiracle. Thereafter, oxygen is obtained from the tracheal system of the host through the anal spiracles, which are pushed tightly backward against the place of attachment. Thus, the caudal end of the body is attached while the cephalic end lies free within the body cavity of the host.

At the end of the third instar, the larvae, then being full grown, leave the host for pupation. The pupal stage may be passed in bark crevices, in the webs of some host like the tent caterpillar or the brown-tail moth, or in the surface layers of the soil. As is the case with most of the other Diptera, Compsilura pupae are

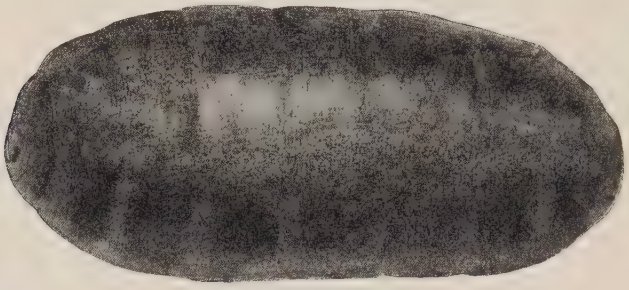


FIG. 157.—Puparium of the tachinid fly, *Compsilura concinnata*. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

enclosed in puparia and not in cocoons. A puparium is the dry, brown, larval skin of the last instar larva (Fig. 157).

Compsilura concinnata is active from the beginning of May to the last of October. During this period, they pass through three, somewhat overlapping, generations. The first adults that emerge in the spring must, as a rule, depend for host material upon caterpillars of species that overwinter in the larval stage. One such species is the brown-tail moth. A little later, in May and June, caterpillars that have hatched from overwintering eggs become available. Among these are the gypsy moths and the tent caterpillars. These insects serve as hosts for the overwintering generation of the parasite. The second-generation adults appear in late June and July. They find a great variety of hosts available (Webber and Schaffner, 1926). The third-generation adults of Compsilura emerge in August and September. At that time, comparatively few host species are available. Doubtless, this condition limits the number of the parasites.

From the preceding discussion it is evident that the host relations of this parasite are exceedingly important in determining its effectiveness in insect control. If secondary hosts are present in adequate numbers to make possible the maintenance of correspondingly large numbers of the parasite, it will be effective. If at any time during the active season the number supply of secondary hosts should fail, then the numbers of the parasite would be so reduced that it might not be effective at other seasons even when hosts were abundant. The critical period for Compsilura appears to be during the third, or overwintering, generation.

CHAPTER XVII

INSECTIVOROUS PREDATORS

It has already been seen that representatives of insectivorous predators are to be found in many different groups of animals. To discuss all these would be far beyond the scope of this book. Consideration, therefore, will be confined to some of the more important of them.

PREDATORY INSECTS

It is impossible to say which of the insectivorous predators are the most valuable from man's viewpoint, but it can be said, without fear of contradiction, that some of the most important of them are insects. The predatory insects are found in a number of different families in several orders. Some of the most effective in the forest are members of the Chrysopidae, the Coccinellidae, the Cleridae, the Carabidae, and several families of the Hemiptera. Important examples of these families will be discussed in the following pages.

The Lacewing Flies.—Members of the family Chrysopidae, of the order Neuroptera, are commonly called *lacewing flies* (Fig. 158). These insects are predaceous in both the larval and the adult stages upon other small insects. They are especially fond of aphids, but they also eat scale inspects, small caterpillars, and other small arthropods. It is only because larger insects are able to defend themselves against attack that they do not fall prey to lacewing flies.

These predators are useful as destroyers of aphids, especially when outbreaks of these insects occur late in the season. Unfortunately, the lacewing flies are not sufficiently numerous in the early part of the summer to be of much aid in reducing the number of other insects at that time of year. As the season advances they become more and more numerous.

The rapid increase in the number of the lacewings, as the season advances, is made possible by the short life cycle of some

of the more common species. Some of them pass through three or four generations during a season. Other species, however, do not multiply so rapidly. In fact some may pass through only one generation during a year. The latter species are, of course, not important predators, because they never become very numerous.

The adult lacewing fly is a slender fragile-appearing insect, about ½ inch in length, with delicate, many-veined, membranous wings. The wings, when at rest, are folded against the body and meet over the insect's back in a form resembling a tent. The adults present anything but the appearance of predators. The larvae, on the other hand, look quite ferocious. They are elongate, somewhat flattened, and have a pair of long, curved mandibles projecting forward from the mouth. These mandibles are hollow, and it is through them that the insect sucks the blood of its prey.

FIG. 158.—A lacewing-fly larva feeding upon an aphid. (*Cornell University.*)

The habits of the lacewing flies present a number of interesting features, the first of which is the habit of oviposition (Smith, 1922). When a female lacewing is ready to lay an egg, she touches her abdomen to the surface of the leaf or other object on which she is resting. A drop of viscous fluid exudes from the end of her abdomen. Then she pulls the drop of liquid out into a slender thread by raising her abdomen. The thread quickly hardens in an erect position and on the top of it an egg is deposited. In this way, the eggs are held almost ½ inch above the surface to which they are attached. This method of placing the eggs on a stalk raises them out of reach of the cannibalistic lacewing larvae and other predaceous insects.

When the larvae hatch from the eggs, they immediately start out in search of food. Almost any insect that is small enough to be held is attacked, impaled upon the mandibles, and drained of its blood. When food is abundant and temperature conditions are favorable, the larvae grow rapidly. They molt twice before they complete their growth.

When the third instar larvae are full grown, they spin about themselves a light silken cocoon. The cocoons may be located in a bark crevice, on the lower side of a leaf, or in some other more or less secluded location. Within the cocoon the larva passes

through a prepupal stage before transforming to the pupal stage. During the summer months, the pupal stage is completed in several weeks. When pupation occurs in the autumn, on the other hand, the pupal stage continues over winter and the adult does not emerge until early the following spring.

The lacewing flies, because of their good work in destroying aphids, are generally very beneficial insects. In some instances, however, their predaceous proclivities are not so much to be desired. Occasionally, they may attack and kill the larvae of coccinellids or other beneficial organisms. But inasmuch as this usually occurs only when aphids, scales, or other small insects pests are not numerous, it is not so serious as it might otherwise be.

The Ladybird Beetles.—The Coccinellidae are members of the order Coleoptera. They are for the most part predaceous. The adults of this family are called *ladybird beetles* (Fig. 159). Like the lacewing flies, these insects are predaceous upon small insects in both the adult and the larval stages. Aphids or scale insects are their usual prey, but they will feed upon small caterpillars, mites, or almost any small organism that they may find. In one instance, a comparatively large coccinellid, the fifteen-spotted ladybird beetle, *Anatis ocellata*, was partly responsible for checking an outbreak of the spruce budworm on jack pine.

The life cycle of the ladybird beetles, as might be expected, varies somewhat with the species. Many of them have two or more generations even in northern latitudes, while in the South a still greater number may be completed. The insects pass the winter in the adult stage, hidden away in some protected location. Many of them may creep into buildings for the purpose of hibernating. When spring arrives, the beetles leave their winter quarters and seek out suitable places for oviposition. The eggs are laid in a variety of ways, depending upon the species. One of the California ladybirds, *Rhizobius ventralis*, deposits its eggs beneath the scale of the black-scale insects. The larvae that hatch from these eggs feed upon the eggs of the scale (Quayle, 1911).

Some of our more common native species deposit their eggs in groups on the surface of the foliage upon which their prey feeds. The eggs are usually yellow and resemble somewhat those of some of the chrysomelids, the leaf beetles. The larvae that

hatch from these eggs are campodeiform and active. Immediately after hatching, they begin to search for food. These larvae are strange-looking creatures. Many of them are mottled with contrasting colors and are covered with branched spines. Their

FIG. 159.—The four stages in the development of a ladybird beetle from egg to adult. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

mandibles are long and sharp so that they are well equipped to capture small insects.

After the larvae complete their growth they transform, usually on the tree, to the pupal stage. These pupae are naked and are often found in very conspicuous places. Apparently most of these insects make no effort to seek a secluded place for pupation. The beetles that emerge from the cocoons during the summer lay eggs immediately for another generation, whereas those that

emerge in the autumn seek out a suitable place for hibernation and there spend the winter.

The Checkered Beetles.—The family of beetles known as the Cleridae is made up of species that are predaceous, for the most part, upon insects that tunnel into the bark, wood, or tips of trees. The most common species in eastern United States is called the *American bark-beetle destroyer, Thanasimus dubius.* This species feeds almost exclusively upon various species of bark beetles.

The bark-beetle destroyer is large for a clerid. It measures nearly ½ inch in length. It is very brightly colored. The ground color is red, and on this background are markings of black and silver in transverse bands across the elytra. This type of marking is characteristic of the group and is the basis for the common name of the family, the *checkered beetles.* These insects are predaceous in both adult and larval stages. The adult preys upon adult bark beetles, whereas the larvae feed upon the immature stages.

The eggs are deposited in the tunnels of bark beetles. The larvae are more or less grub-like in form with poorly developed legs but with powerful mandibles. They are usually pinkish in color. The larvae are not at all uncommon beneath the bark of trees infested by bark beetles. They feed upon both eggs and larvae. When they are numerous they materially reduce the bark beetles in number. When they complete their development the larvae cut their way into the outer bark. There they hollow out cells for themselves in which they pass through the pupal stage (Fig. 160).

According to Hopkins (1899), this insect may pass the winter in any stage of development from larva to adult. In the spring, the beetles emerge in time for the spring flight of the bark beetles. They may run rapidly over the surface of trees and logs looking for their prey, or they may hide beneath a bark scale waiting to pounce out upon any unfortunate bark beetle that may pass by.

One of the commonest and perhaps the most important of the Western species of clerids is *Enoclerus sphegeus.* It feeds actively on adults and larvae of various bark beetles and has attracted especial attention by its attacks on dendroctonus beetles.

The Calosoma Beetles.—The ground beetles, or carabids (Fig. 161), belonging to the genus Calosoma are among the

important predators of lepidopterous larvae and pupae. The habits of these beetles have been studied in great detail in con-

FIG. 160.—Prepupal larva of a clerid *Thanasimus nigriventris* in a cell under a scale of ponderosa pine bark. (*Bureau of Entomology and Plant Quarantine, U. S. Dept. Agr.*)

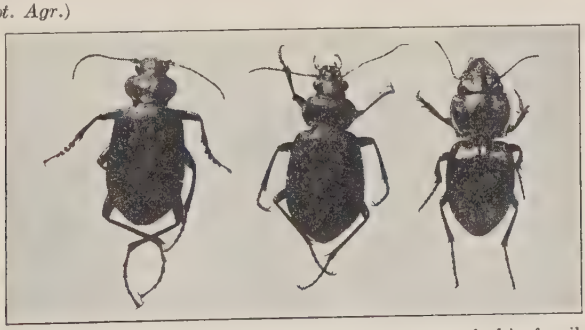


FIG. 161.—Three typical carabid beetles. The beetles of this family are predaceous in both adult and larval stages. (*University of Minnesota.*)

nection with the gypsy-moth investigations in New England (Burgess and Collins, 1917). The beetles of this group are among the largest of the ground beetles.

In a general way, the life cycle of the calosoma beetles is very similar for all the species that have been studied. The eggs are deposited in the ground at a depth of from 4 to 6 inches, either singly or in groups of two or three. After an incubation period of from 3 to 15 days, the eggs hatch and the larvae make their way upward to the ground surface, where they proceed to search for food. They prefer lepidopterous larvae, but they will eat other insects if forced to do so by hunger.

At the end of the third instar the larvae have completed their growth. Then they again penetrate into the soil where they form for themselves earthen cells in which to pupate. After from 10 to 15 days in these cells the adult stage is attained.

Some species, as soon as they have transformed to the adult stage, emerge and feed during the latter part of the summer and autumn. Later they again bury themselves in the ground for hibernation. Others, like the fiery hunter, remain in the young adult stage within their pupal cells until the following spring. So far as is known, all the calosoma beetles are unusually long lived. Burgess and Collins (1917) report that in the field they may undoubtedly live, unless they meet with some accident, for at least 3 years. They report that one adult fiery hunter has lived for more than 4 years. Those beetles that lay eggs freely during their early life do not live so long as others that do not reproduce so freely.

Both the adults and the larvae of the fiery hunter feed upon lepidopterous caterpillars. The species eaten will, of course, vary with the season and will depend upon the species available when feeding is going on. In New England the gypsy moth is a favorite prey. The adult beetles will climb the trees in search of food, but the larvae of most species feed almost exclusively upon the ground. One outstanding exception to this is the fiery hunter. This insect climbs trees in both the adult and larval stages and is, therefore, a much more efficient factor of environmental resistance than any of our native species of the genus.

The Predaceous Bugs.—The order Hemiptera, in addition to the numerous species that suck the sap of trees, includes a great many predaceous species. These predaceous forms are found in a number of different families. All the members of the family Reduviidae, or assassin bugs, are predaceous, and most of them are predaceous upon insects. One of the well-known members of

this family is the wheel bug, *Arilus cristatus*. This insect is common throughout the eastern and central United States south of the latitude of New York City (Fig. 162).

The wheel bugs lay their eggs upon plants or other objects in groups of 50 or even more. The young nymphs that hatch from these eggs are bright red with rather long legs and long four-

FIG. 162.—The various stages of the wheel bug, *Arilus cristatus*. (*Comstock "An Introduction to Entomology."*)

jointed antennae. They run about over plants seeking insect food. In the early stages they feed for the most part upon aphids and other small insects. As they increase in size they feed on larger insects. When they are full grown they are ¾ inch in length and are able to attack and kill insects of considerable size.

Another family of the Hemiptera that contains predaceous species is the family Pentotomidae. Some species of this family feed upon the juices of plants, but many suck the blood of other insects during at least a part of their lives. These predaceous species are often called soldier bugs.

One of these soldier bugs is *Podisus placidus* (Fig. 163). When in the adult stage, this predator is nearly ½ inch in length and

in color, yellow mottled with brown. It is predaceous upon many different species of caterpillars. Felt (1906) records the following species as being fed upon by this insect: the tent caterpillars, the pine sawfly, the senatorial oak-caterpillar, the currant worm, the spiny elm-caterpillar, the fall webworm, the white-marked tussock-moth, and the gypsy moth.

The winter is passed by *Podisus placidus* in the adult stage. The overwintering adults appear in the early spring and after feeding for a week or two lay their eggs in groups on the underside of leaves or in other convenient places. When the young nymphs emerge, they are red and black in color. Unlike the adults and older nymphs, the young nymphs are not predaceous. Instead, they are phytophagous and feed upon the plant juices that they suck from the leaves of trees or shrubs. Not until they have lived on a vegetable diet for a period of about 2 weeks do they adopt the predaceous habit. Then, by destroying numerous harmful insects, they more than compensate for the insignificant amount of injury that has resulted from their feeding on the leaves. The soldier bug has two generations in the North. In the South it may have still more. Several other families of the Hemiptera are predaceous upon insects, but none of them are as valuable predators of forest insects as the two discussed above.

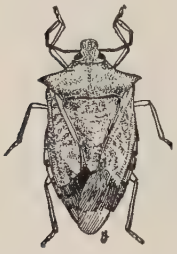


FIG. 163.—The spined soldier-bug, *Podisus maculiventris*. This species feeds upon a great variety of other insect species. (*Felt, Manual of Tree and Shrub Insects.*)

OTHER PREDATORS

In addition to the insect predators discussed in the preceding section, there are a number of other groups of insectivorous predators that should at least be touched upon briefly. Among these are some other arthropods.

Arthropods Other than Insects.—Among the organisms that prey upon insects, the spiders and the mites should not be overlooked. It is a matter of common knowledge that spiders are highly insectivorous. They not only catch flies and certain other more or less innocuous insects, but they also feed upon small larvae of various kinds. The spiders that spin webs frequently capture larvae that drop on threads and are

blown about by the wind. Those spiders that actively hunt their prey are probably even more effective in the capture of larvae.

Strange as it may seem, however, no one has published the results of any quantitative study concerning the effectiveness of these animals. It must be admitted, however, that spiders must exert a tremendously important influence upon the insect life in the forest. The study of the effects of spiders upon forest insects offers a fertile field for future investigators.

Likewise, when the literature is examined for facts concerning the predaceous mites, a decided shortage of information is found. One of the few that has been studied is the egg-destroying mite, *Hemisarcoptes malus* (Fig. 164), which exercises an important controlling influence upon the oyster-shell scale (Tothill, 1918). In some localities this mite is the most effective single biotic factor of environmental resistance. Doubtless, many other predaceous mites play an equally important role, but, unfortunately, comparatively little is known about them.

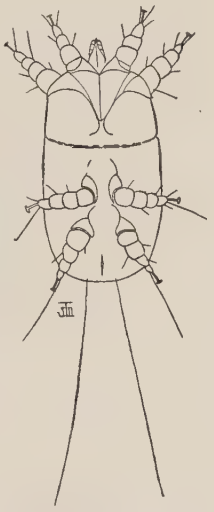


FIG. 164.—The predaceous mite, *Hemisarcoptes malus*, one of the important enemies of the oyster-shell scale. (*Entomological Branch, Can. Dept. Agr.*)

Insectivorous Vertebrates.—Another group of organisms that has already been mentioned as being insectivorous is the Vertebrata. Some workers believe that this group contains some of the most effective insectivorous animals. Whether or not they are the most effective can only be a matter of conjecture until accurate quantitative data are secured on which to base a conclusion, but there can be no doubt that these organisms play an important part in holding down insect numbers.

General observation is sufficient to indicate that skunks, shrews, mice, and other mammals destroy great quantities of insects on or in the ground. It has been shown that mice and shrews are, at least in certain years and in certain localities, many times more effective in reducing the abundance of the larch sawfly during the cocoon stage than all the parasites combined (Graham, 1928).

But of all the vertebrates, the birds are probably the most important insect eaters. McAtee (1926) mentions numerous instances in which birds have brought insects under control. He cites the elm spanworm (snow-white linden-moth) which once was exceedingly injurious to shade trees. With the introduction and establishment of the English sparrow in the cities and towns of this country, the elm spanworm has become a rare insect. Instances are cited in which birds have destroyed from 15 to 89.5 per cent of all the fall-webworm larvae in certain localities (Tothill, 1922). In a study of the natural agencies that control the white-marked tussock-moth, Dustan (1923) reports that almost every egg mass above the snow line was either partially or wholly destroyed by birds. This amounted to 90 per cent of the egg masses. The cankerworms, the tent caterpillars, the gypsy moth, in fact practically every kind of leaf-eating insect is fed upon by many species of birds.

Most of the instances cited in literature in which birds have brought insect outbreaks under control have been in connection with sporadic or local outbreaks. Obviously the limitations in reproductive rate and the territorial limitations of most birds will prevent them from becoming sufficiently numerous to check a widespread outbreak. This is brought out by Strickland (1928), who reaches the conclusion that because of these characteristics birds cannot play an important part in insect control.

The fallacy in his argument is that he fails to recognize the importance of birds, working along with other factors of environmental resistance, when the insects are present in normal numbers. By these activities they may be very effective in reducing the amplitude of the oscillation of prey numbers about the mean and thereby may reduce the danger that excessive population fluctuations will occur as a result of reduced physical resistance. This relationship is discussed further in Chap. V.

Many birds are highly insectivorous throughout their lives. The swallows, martins, and nighthawks are among these. Others are more or less omnivorous like the crows, blackbirds, thrushes, and gallinaceous birds. Almost all the songbirds, including even the finches, that are usually thought of as being seed eaters, are highly insectivorous in the nestling stage. Because these birds are nesting during the period of greatest insect abundance they are especially valuable aids in holding down insect populations.

Even the birds which are usually considered as being phytophagous are, almost without exception, insectivorous during the nestling stage. The fact that the nesting season of most birds coincides with the season of greatest insect abundance leads to a great abundance in number of insect-eating birds during that season. Undoubtedly, the ability of many species of birds to change from insect to plant food, and vice versa, makes it possible for more birds to live in a locality than if they all fed throughout the season on one type of food. When insect food is abundant,

FIG. 165.—The blackburnian warbler. A bird that has proved itself to be a very effective check upon the spruce budworm. (*University of Minnesota.*)

the birds concentrate their attention upon that. Later, when insects become scarce, fruit and seed are plentiful and provide food for birds. In this way, the bird population is able to maintain itself, throughout the season, in sufficient numbers to make them effective agencies for controlling insects.

Practically every species of insect has its bird enemies in almost every stage. The eggs are eaten by small birds: nuthatches, chickadees, the brown creeper, warblers, and kinglets, for example. The larvae are fed upon by almost every species of bird (Fig. 165). The pupae likewise are searched out and eaten, even though they may be enclosed in strong cocoons.

Even the boring insects are not without their bird enemies. The woodpeckers are most valuable in destroying these insects, as they bore for food beneath the bark or even into the wood. When the adults of the borers fly from their old tunnels to a new host, they are subject to the attack of a long list of birds. Fly catchers, the crow, jays, the bluebird, swallows, night-

hawks, in fact, a long list of 100 or more species, feed upon adult borers.

Birds are sometimes especially effective in checking sporadic outbreaks in part because of their great powers of mobility. This permits them to concentrate in those places where insects are most numerous. Because of this ability many incipient insect outbreaks are checked by these valuable predators.

CHAPTER XVIII

OTHER RELATIONS OF FOREST INSECTS

SOME INDIRECT EFFECTS OF FOREST INSECTS

Forest insects, in addition to the direct effects in killing trees, reducing their growth rate, and injuring their products, may exert indirect influences upon the forest that will be considered in this chapter. These effects are sometimes very complex and frequently imperfectly understood. The purpose of this chapter, because of the paucity of available information on this subject, is primarily intended to introduce the subject and show some of its possibilities. Some of these indirect effects, although their importance is fully realized, will only be mentioned; for instance, the influence of insects in aerating and turning over the soil is obviously of major importance. In Darwin's classical treatise on the earthworm, ants might very appropriately have been substituted for earthworms as the workers of the soil. Obvious likewise is the ecological importance of duff-eating insects and insects that eat decaying wood. Their activities hasten the conversion of dead vegetation to soluble chemical compounds that can be used by green plants. Likewise the part that insects play in the fertilization of flowers is an important subject. But this discussion of indirect effects will be along other lines and will be concerned with those influences that involve the immediate health of individual trees or the marketability of their products. Some of them have been mentioned casually in previous chapters.

Insects as Transporters of Other Insects.—How a relatively nonmotile insect, like a scale insect, can be carried from tree to tree is a question that cannot be easily answered. The transfer must usually occur during the brief periods when they are moving from place to place. It is said that they may be blown from tree to tree by wind. But observations of newly hatched scales seem to indicate that they cling tightly to the surface on which

they find themselves as they move slowly about in search of a suitable place to insert their beaks. Certainly they would not easily be blown away under normal circumstances.

Therefore we are forced to conclude that scales are usually moved from tree to tree by agencies other than wind. It is thought that they may crawl upon the feet of birds and thus be moved from place to place. This could easily happen if the bird flew with his passengers to a suitable species of tree and sat quietly until they disembarked. Doubtless this does occur. But if it does, it seems equally likely that the young scales may make similar use of other insects. Thus winged insects may serve unwittingly in transporting small wingless insects of another species from one tree to another.

This possible spreading of scales by larger insects may be a matter of conjecture, but it is definitely known that in some instances insects intentionally transport insects of another species from place to place. Ants are frequently responsible for moving aphids and mealybugs from one location to another. This is a part of a definite symbiotic relationship which has doubtless developed from the common and very simple situation where the ants attend and in some instances protect naturally established colonies of sucking insects for the honeydew that they excrete.

Illustrations of highly developed symbiotic relationships between ants and sucking insects are more commonly known in the field of agriculture than in forestry, but this is probably due to the greater intensity of study that agricultural crops have received. One illustration that is frequently cited is the relationship of the field ant and the corn-root aphid. In this case the aphid is practically dependent upon the ants for its existence, and anything that reduces the number of ants also reduces the aphid population.

These aphids are placed on the roots of the corn in the spring, possibly moved from unfavorable to more favorable locations as the season progresses, and finally taken into the ant nest to overwinter.

Another agricultural illustration of a somewhat similar situation is that of the pineapple mealybug and ants in the Hawaiian Islands. There the ants are primarily responsible for carrying the mealybugs from plant to plant. In this activity they tend

to move along a row from one plant to the next. This habit has led to the development of a simple but ingenious procedure that is helpful in controlling the mealybugs. By encircling the field with several rows of plants, instead of running the regular rows to the edge of the field, the ants are discouraged from carrying the mealybugs into the field.

Keen (1938) reports that the carpenter ant has been known to shelter aphid eggs in its nest during the winter and in the spring transfer them to the trees on which they develop. The reward that the ants receive for this attention is a supply of honeydew that is excreted by the aphid from the anal opening. This is a prized article of ant diet.

Insects and Wood Rot and Stains.—Wood-rotting organisms doubtless gain entrance into wood in a variety of ways, but undoubtedly insects are an important means of accomplishing inoculations. This may be brought about either directly or indirectly. In the first instance the insects carry the inoculum into the wood when they make their initial attack. In the second instance the fungus gains entrance without aid of the insects, through the openings made by the insects.

Bark beetles as a group almost invariably inoculate with fungi the trees that they attack, the spores of which are carried into the tree on their bodies (Leach, 1934). Some of these fungi are wood stainers, and others cause decay. In addition to the inoculum carried with them, these insects keep their burrows clear or at least partly clear of frass, and they keep the entrance holes open during the active life of an attack. Thus the way is kept open for accidental inoculation by a variety of means.

The interrelation of various species of dendroctonus beetles, but particularly the southern pine-beetle with blue-stain organisms, has received much study and is now well known. Although the insects do not depend in any direct way upon the fungus, their bodies are invariably contaminated, and therefore an attack by these beetles is invariably accompanied by an infection of blue-stain fungi. The fungous infection, as previously indicated, invades and obstructs the conducting tissues of the tree, thus materially hastening its death (Nelson, 1934; Craighead, 1928).

Wood borers like various species of Monochamus, Saperda, and carpenter worms keep their galleries partly clear of frass. In the

tunnels of these insects, fungous infection almost universally occurs. Sections of logs infested by these insects will often clearly show discoloration caused by rotting fungi near the insect tunnels, the focus of the infection being unmistakable.

In all these instances the insects have merely opened the way for infection into locations already suitable for fungus growth, but in other instances the insects may improve conditions for decay; for instance, carpenter ants and termites are usually associated with decay and by their activities in the wood both open the way for inoculation and also maintain in their nests favorable conditions of moisture for fungous growth. It also seems likely that termites, in extending their tunnels from a piece of rotting wood to sound timber, may actually carry the infection with them. The source of nitrogen in the diet of termites has puzzled physiologists. Perhaps one source of this element may be found in the fungous hyphae which they ingest with the wood that they eat.

Insects and Parasitic Fungi.—Not infrequently insects are responsible for the transmission of parasitic fungi. It has been demonstrated that the gypsy-moth larvae are potential carriers of white-pine blister-rust. The newly hatched larvae may feed upon the spore pustules on white pine and then inoculate Ribes, on which they may later feed (Gravatt, 1918). This method of inoculation is probably of minor importance practically, but indicates how such fungi may be transmitted from plant to plant by the aid of insects.

Many years ago it was demonstrated that insects might carry the inoculum of the chestnut blight from tree to tree (Ruggles, 1913).

Very recently the establishment of the Dutch elm-disease in the eastern United States has brought into greater prominence than ever before the importance of insects as vectors of disease-causing organisms. It has now definitely been demonstrated that the small European elm bark-beetle, *Scolytus multistriatus*, and the native elm bark-beetle, *Hylurgopinus rufipes*, are able to carry the inoculum of the Dutch elm-disease from one tree to another.

Both of these insects attack sick and dying elms and are almost always found in elms that have been killed by the Dutch elm-disease. In this way many become contaminated with the

fungus. If they confined their attack to sick or dying trees, the effects would not be serious. But unfortunately both of these beetles have the habit of cutting feeding tunnels in the bark of apparently healthy elms (Kaston, 1938; Martin, 1938), and, although they rear no brood in them, they may infect these healthy trees with the disease.

The seriousness of this habit is self-evident, because it increases many times the chances of infecting healthy trees. It also emphasizes the importance of the point made by Felt (1935) that strenuous efforts should be made to reduce the population of elm beetles by immediately cutting and burning all dead, sickly, or dying trees in or near the infected areas. This problem of sanitation in some localities infected by the Dutch elm-disease has been greatly complicated and made more difficult as a result of the damage caused by the 1938 hurricane. Unless the wind-thrown elms are barked, utilized, or stored in water there will inevitably be a tremendous increase in elm bark-beetles.

Felt has also demonstrated that such insects as the elm beetles may be caught in convection currents and carried for long distances beyond the limits of normal flight, perhaps for hundreds of miles.

It has also been shown that the Dutch elm-disease develops slowly in a tree after infection and may not make itself evident externally for a number of years. Thus there is always the danger that beetles may become contaminated from trees that are apparently healthy and spread infection therefrom, even though all trees visibly infected in a locality are promptly cut.

Therefore the possibility of eradicating this disease from the United States seems highly problematical. For this reason it would seem especially wise to follow the advice of Felt and take steps to reduce the population of the two most important insect carriers of the disease, not only in the infected localities but in all localities where elm is an important tree, since the spread of the disease seems to depend primarily on elm insects. To accomplish this, state and municipal governments and private individuals must cooperate to remove and destroy not only the sick, dead, and dying trees, but also to remove dead, dying, or injured branches from otherwise healthy trees. It seems possible that by such a procedure it may be possible to save the elms, even though the disease becomes generally distributed.

Insects and Virus Diseases.—The so-called *virus diseases* have been responsible for heavy losses to agricultural crops including some woody plants, but they have seldom been considered in forestry. It seems likely, however, that they do occur much more frequently than they have been recognized. It is possible that some of the so-called *leaf blights* and other similar troubles that are usually classed as physiological may belong to this group of diseases.

Many of the so-called *leaf burns* of herbaceous crops and various mosaic diseases of both herbaceous and woody plants belong in this class. Almost all these diseases are transmitted from plant to plant by sucking insects.

Sometimes it is difficult to determine whether the insect is the direct cause or whether it is associated with a disease-causing virus. Such a case is the flagging disease of pine that is now prevalent in parts of the Southwest and in the East. It causes branch ends to die and the needles to turn red. This particular flagging disease is always associated with a sucking insect belonging to the genus Matsucoccus. Some suspect that the insect merely transmits the disease organism from one pine to another, whereas others suspect the insect of being the primary causal agency. The final answer must await the results of research now under way.

In the case of certain diseases of agricultural crops, the connection between sucking insects and virus diseases has been definitely established. For instance, raspberry mosaic is transmitted from plant to plant by aphids. Potato mosaic and curly top of beets are transmitted by leaf hoppers. Some other mosaic and mosaic-like diseases are transmitted by mealybugs.

This discussion of these indirect effects has been presented more for the purpose of arousing interest in the possibilities of these interrelationships than to present information. Here is a potential field that may undoubtedly be explored with profit.

A GLIMPSE INTO THE FUTURE

In concluding a book of this sort it may be permissible to look toward the future for some indication of what may be in store for the forest entomologist in years to come. Such an examination must of necessity be made with the eyes of the past and with the evident limitations of such a viewpoint.

We have seen forest entomology pass from the stage of simple natural history of forest insects into the stage of experimental and applied biology and ecology. We have seen in the eastern part of the United States the passing of the virgin timber. With its passing there has come a shift of emphasis from the insects that attack the overmature virgin forest to those that are pests of young second-growth timber.

Likewise in the West we may look for a similar change. In fact there are already indications that this change is beginning. The passing of the virgin forest will there, as in the East, bring a shift of emphasis from the insects that injure mature timber to those that affect second growth.

Thus in the future it appears almost certain that bark beetles will assume a position of lesser importance than today and that defoliators will come to hold the center of the stage.

Destructive logging procedures, followed by or accompanied by fires, will pave the way for the development of *fire-type* forests on an unprecedented scale. In other instances absolute protection and selective logging on an individual-tree basis will result in the development of the various climax forest types that are in many instances as susceptible to insect attack as are pure or nearly pure stands that arise as a result of fire. Along with these types will come all the problems that are associated with such forests, and we may expect to see numerous insect species that are now unknown, or looked upon as being unimportant, becoming epidemic and causing inestimable losses.

At present the forest entomologist is being called upon to show how the insect-susceptible second-growth forests of the East may be handled silviculturally in order to avoid the danger of insect damage. Soon a similar situation will undoubtedly arise in the West. The forest entomologist who is lacking in a knowledge of silvics, silviculture, and forest management will be helpless to cope with these problems. Likewise the silviculturist with a limited knowledge of insects and their ways will be at a loss how to make the forest safe from insects. The combined efforts of the silviculturist, the forest manager, and the entomologist will be required to solve the complex ecological problems where forest insects are involved.

But if the entomologist knows little or no silviculture, the forest manager and the silviculturist no entomology, the chance

of reaching a prompt and effective solution of the forest entomological problems of the future will be slim indeed. Thus, in spite of the contention that this is an age of specialization, it seems evident that specialization will fail unless it is built on a broad base, so that the specialist will have an appreciation and understanding of fields closely associated with his own. Thus it follows that the forest entomologist whose entomological training is supplemented by a knowledge of silviculture and forest management will be in demand to work with the silviculturist to rebuild the forests of precarious composition that characterize the present and immediate future forests in the United States.

BIBLIOGRAPHY

Chapter I—Introduction

Banks, N., 1906. "Bibliography of the More Important Contributions to Economic Entomology." vols. 6–8, 1888–1905. (See also Henshaw and Colcord.)

———, 1916. "Index to the Literature of American Economic Entomology," vol. 1, 1905–1914.

Chamberlin, W. J., 1931. "An Introduction to Forest Entomology."

Colcord, M., 1921, 1926. "Index to the Literature of Economic Entomology." vols. 2, 3, 4, and 5, 1915–1919, 1920–1924, 1925–1929, 1930–1934. (See also Banks and Henshaw.)

Comstock, J. H., 1936. "An Introduction to Entomology."

Craighead, F. C., 1930. An annotated list of important North American forest insects, *U. S. Dept. Agr., Msc. Pub.* 74.

Doan, R. W., Van Dyke, E. E., Chamberlin, W. J., and Burke, H. E., 1936. "Forest Insects."

Essig, E. O., 1929. "Insects of Western North America."

Felt, E. P., and Rankin, W. H., 1932. "Insects and Diseases of Ornamental Trees and Shrubs."

Graham, S. A., and A. G. Ruggles, 1923. The obligation that economic entomology owes to forestry, *Jour. Econ. Ent.*, **16**: 51–61.

Hagen, H. A., Horn, W., and Schenkling, S., 1928–9. "Index Literaturae Entomologicae." 4 vols. to 1863.

Henshaw, S., 1888. "Bibliography of the More Important Contributions to American Economic Entomology." vols. 1–5. (See also Banks and Colcord.)

Herrick, Glenn W., 1935. "Insect Enemies of Shade Trees."

Houser, J. S., 1918. Destructive insects affecting Ohio shade and forest trees, *Ohio Agr. Exp. Sta., Bull.* **332**: 161–487.

Keen, F. P., 1938. Insect enemies of western forests, *U. S. Dept. Agr., Msc. Pub.* 273.

Kotinski, J., 1921. Insects injurious to deciduous shade trees and their control, *U. S. Dept. Agr., Farmers' Bull.* 1169.

Lutz, Frank E., 1935. "Fieldbook of Insects."

Packard, A. S., 1890. Insects injurious to forest and shade trees, *U. S. Ent. Comm., Fifth Rept.*

Peirson, H. B., 1927. Manual of forest insects, *Maine Forest Service, Bull.* 5.

Salman, K. A., 1937. The regional survey of forest insect conditions in the California region, 1931–1936, *U. S. Dept. Agr., Bur. Ent. P. Q.*, Berkeley, Calif., May 1, 1937. (Mimeographed publication.)

Snyder, T. E., 1927. Defects in timber caused by insects, *U. S. Dept. Agr., Bull.* 1490.

Swaine, J. M., 1918. Canadian bark-beetles, *Can. Dept. Agr., Ent. Branch, Tech. Bull.* 14.

Swaine, J. M., and Hutchings, C. B., 1926. The more important shade-tree insects of Eastern Canada, *Can. Dept. Agr., Ent. Branch, n. s., Bull.* 63.

Wardle, R. A. and Buckle, P., 1923. "The Principles of Insect Control."

Wardle, Robert A., 1929. "The Problems of Applied Entomology."

Insects that attack tree seeds:

Brooks, Fred E., and Cotton, R. T., 1929. Chestnut curculios, *U. S. Dept. Agr., Tech. Bull.* 130.

Miller, John M., 1914. Damage to cones, *U. S. Dept. Agr., Bull.* 95.

———, 1915. Damage to sugar pine and western yellow pine cones, *U. S. Dept. Agr., Bull.* 243.

———, 1916. Oviposition of *Megastigmus spermotrophus* in Douglas fir seed, *Jour. Agr. Res.*, **6**: 65–68.

Reiss, Donald, 1935. Biological study of the walnut husk fly, *Mich. Acad. Sci., Arts, Letters*, **20**: 717–723.

Chapter II—Historical Review

Nusslin, O., and Rhumbler, L., 1922. "Forstinsektenkunde," pp. 1–9.

Chapter III—Biotic Potential

Chapman, R. N., 1925. "Animal Ecology with Special Reference to Insects," pp. 143–149.

Folsom, J. W., and Wardle, R. A., 1934. "Entomology with Special Reference to Its Ecological Aspects," pp. 123–126.

Graham, S. A., 1926. Biology and control of the white-pine weevil, *Cornell Agr. Exp. Sta., Bull.* 449.

———, 1936. The spruce budworm on Michigan pine, *Univ. Mich., School Forestry Cons., Bull.* 6.

LeFroy, H. M., 1909. "Indian Insect Life," 624.

Thompson, W. R., 1922. Étude de quelques cas simples de parasitisme cyclique chez les insectes entomophages, *Comp. rend. Acad. Sci. Paris*, **174**: 1647–1649.

———, 1922, Théorie de l'action des parasites entomaphages, *Comp. rend. Acad. Sci. Paris*, **175**: 65–68.

Chapter IV—Environmental Resistance

Baumberger, J. P., 1919. A nutritional study of insects with special reference to micro-organisms and their substrata, *Jour. Exp. Zool.*, **28**: 1–81.

Blackman, M. W., 1918. The American tent-caterpillar, *Jour. Econ. Ent.*, **9**: 432.

CARPENTER, F. W., 1909. Some reactions of Drosophila, *Jour. Comp. Neurol.* and *Psych.*, **18**: 483–491.

CRAIGHEAD, F. C., 1921. Hopkins' host-selection principle as related to certain cerambycid beetles, *Jour. Agr. Res.*, **22**: 189–220.

———, 1925. Relation between mortality of trees attacked by spruce budworm and previous growth, *Jour. Agr. Res.*, **30**: 541–555.

CHAPMAN, R. N., 1915. Observations on the life history of *Agrilus bilineatus*, *Jour. Agr. Res.*, **3**: 283–294.

———, 1925. "Animal Ecology with Special Reference to Insects," pp. 149–158.

COOK, W. C., 1927. Some effects of alternating temperature on growth and metabolism of cutworm larvae, *Jour. Econ. Ent.*, **20**: 769–782.

———, 1929. A bioclimatic zonation for studying the economic distribution of injurious insects, *Ecology*, **10**: 282–293.

GRAHAM, S. A., 1920. Factors influencing the subcortical temperature of logs, *Minn. State Ent. Rept.*, **18**: 26–42.

———, 1922. Effect of physical factors in the ecology of certain insects in logs, *Minn. State Ent. Rept.*, **19**: 22–40.

———, 1924. Temperature as a limiting factor in the life of subcortical insects, *Jour. Econ. Ent.*, **17**: 377–383.

———, 1926. Biology and control of the white-pine weevil, *Cornell Agr. Exp. Sta., Bull.* 449.

HODSON, A. C., 1937. Some aspects of the role of water in insect hibernation, *Ecological Monographs*, **7**: 271–315.

HOLDAWAY, F. G., and SMITH, H. F., 1933. Alteration of sex ratio—following starvation of newly-hatched larvae, *Australian Jour. Exp. Biol. Med. Sci.*, **11**: 35–43.

HOPKINS, A. D., 1920. The bioclimatic law, *Jour. Wash. Acad. Sci.*, **10**: 34–40.

———, 1921. Bioclimatic zones determined by meteorological data, *U. S. Dept. Agr. Weather Rev.*, **49**: 229–330.

———, 1921. Bioclimatic zones of continents with proposed designations and classification, *Jour. Wash. Acad. Sci.*, **11**: 227–229.

———, 1938. Bioclimatics, *U. S. Dept. Agr., Msc. Pub.* 280.

HOWARD, L. O., 1926. The parasite element of natural control of injurious insects and its control by man, *Jour. Econ. Ent.*, **19**: 271–282.

KEEN, F. P., 1937. Climatic cycles in eastern Oregon as indicated by tree rings, *U. S. Dept. Agr. Weather Bur., Weather Rev.*, **65**: 175–188.

KEEN, F. P., and FURNISS, R. L., 1936. Effects of subzero temperatures on populations of the western pine beetle, *Jour. Econ. Ent.*, **30**: 482–504.

KROGH, A., 1914. The quantitative relation between temperature and standard metabolism in animals, *Intern. Zeitschr. Physik-Chem. Biol.*, **1**: 491–508.

———, 1914. On the influence of temperature on the rate of embryonic development, *Zeitschr. Allge. Physiol.*, **16**: 163–167.

———, 1914. On the rate of growth and CO_2 production of chrysalides of *Tenebrio molitor* at different temperatures, *Zeitschr. Allge. Physiol.*, **16**: 178–190.

Mail, G. A., 1930. Winter soil temperatures and their relation to subterranean insect survival, *Jour. Agr. Res.*, **41**: 571–591.

Merriam, C. H., 1898. Life zones and crop zones in the United States, *U. S. Dept. Agr. Biol. Survey, Bull.* 10.

Miller, J. M., 1931. High and low lethal temperatures for the western pine beetle, *Jour. Agr. Res.*, **43**: 303–321.

———, 1932. A record of winter kill of western pine beetle in California, 1932, *Jour. Forestry*, **31**: 443–446.

Patterson, J. E., 1927. The relation of highway slash to infestations by the western pine beetle in standing timber, *U. S. Dept. Agr., Tech. Bull.* 3.

Payne, N. M., 1926. Freezing and survival of insects at low temperatures, *Quart. Rev. Biol.*, **1**: 270–282.

———, 1926. The effect of environmental temperatures upon insect freezing points, *Ecology*, **7**: 99–106.

Peairs, L. M., 1927. Some phases of the relation of temperature to the development of insects, *W. Va. Agr. Exp. Sta., Bull.* 208.

Pierce, W. D., 1916. A new interpretation of the relationships of temperature and humidity to insect development, *Jour. Agr. Res.*, **5**: 1183–1191.

Prell, H., 1924. "Über die Immunität von Fichten gegen Nonnenfrass und ihre Ursache," *Tharanter Forstl. Jahrb.*, **LXXV**, no. 2, Berlin.

Robinson, Wm., 1927. Water-binding capacity of colloids a definite factor in winter hardiness of insects. *Jour. Econ. Ent.*, **20**: 80–88.

Salt, R. W., 1936. Studies on the freezing process in insects, *Univ. Minn. Agr. Exp. Sta., Tech. Bull.* 116.

Sanderson, E. D., 1908. The relation of temperature to the hibernation of insects, *Jour. Econ. Ent.*, **1**: 56–65.

Sanderson, E. D., and Peairs, L. M., 1913. The relation of temperature to insect life, *N. H. Coll. Agr. Exp. Sta., Tech. Bull.* **7**.

Snyder, T. E., 1926. Preventing damage by lyctus powder-post beetles, *U. S. Dept. Agr., Farmers' Bull.* **1477**: 1–13.

Snyder, T. E., and St. George, R. A., 1924. Determination of temperatures fatal to the powder-post beetle—in a kiln, *Jour. Agr. Res.*, **28**: 1033–1038.

Summers, J. N., 1922. Effect of low temperature on the hatching of gypsy-moth eggs, *U. S. Dept. Agr., Bull.* 1080.

Uvarov, B. P., 1929. Weather and climate in their relation to insects, *Conf. Empire* (Gt. Brit.) *Meteorologists, Agr. Sec.*, 1929.

Chapter V—Insect Abundance

Chapman, R. N., 1925. "Animal Ecology with Special Reference to Insects," pp. 143–158.

Chapman, R. N., King, K. M., Emerson, A. E., Smith, H. S., and Graham, S. A., 1939. Symposium on insect populations, *Ecological Monographs*, 1939.

Cook, W. C., 1929. A bioclimatic zonation for studying the economic distribution of injurious insects, *Ecology*, **10**: 282–293.

Elton, C. S., 1927. "Animal Ecology."
Folsom, J. W., and Wardle, R. A., 1934. "Entomology," Chaps. VI, XII, and XIII.
Gerould, J. H., 1916. Mimicry in butterflies, *Amer. Nat.*, **50**: 184–192.
Poulton, E. B., 1890. "The Colours of Animals."
Punnett, R. C., 1915. "Mimicry in Butterflies."
Smith, H. S., 1935. The role of biotic factors in the determination of population densities, *Jour. Econ. Ent.*, **28**: 873–898.

Chapter VI—Direct Control of Tree Insects

Balch, R. E., 1937. Notes on the fall cankerworm and the effectiveness of banding, *Rept. Ent. Soc. Ont.*, **1937**: 1–5.
Compere, H., and Smith, H. S., 1932. The control of the citrophilus mealybug, *Pseudococcus gahani*, by Australian parasites, *Hilgardia*, **6**: 585–618.
Craighead, F. C., 1920. Direct sunlight as a factor in forest insect control, *Proc. Ent. Soc., Wash.*, **22**: 106–108.
———, 1921. Temperatures fatal to larvae of the red-headed ash-borer, *Jour. Forestry*, **19**: 250–254.
———, 1921. Protection of mesquite cordwood and posts from borers, *U. S. Dept. Agr., Farmers' Bull.* 1197.
Graham, S. A., 1920. Factors influencing the subcortical temperatures of logs, *Minn. State Ent., Rept.*, **18**: 26–42.
Hoffmann, Chr., 1937. Nonnenfalter kontrolle auf biologischer Grundlage, *Forstwiss. Centralbl.*, **59**: 549–551.
Jones, D. W., 1926. Some notes on the technic of handling parasites, *Jour. Econ. Ent.*, **19**: 311–316.
Metzger, F. W., 1935. Traps for Japanese beetles and how to use them, *U. S. Dept. Agr., Msc. Pub.* 201.
Patterson, J. E., 1930. Control of the mountain pine beetle in lodgepole pine with solar heat, *U. S. Dept. Agr., Tech. Bull.* 195.
Smith, H. S., 1921. Biological control of the black scale, *Jour. Econ. Ent.*, **14**: 348–350.
———, 1925. The commercial development of biological control in California, *Jour. Econ. Ent.*, **18**: 147–152.
———, 1926. The present status of biological control work in California, *Jour. Econ. Ent.*, **19**: 294–302.
Turner, W. B., 1918. Female Lepidoptera at light traps, *Jour. Agr. Res.*, **14**: 135–149.
———, 1920. Lepidoptera at light traps, *Jour. Agr. Res.*, **18**: 475–481.
Wardle, R. A., and Buckle, P., 1923. "The Principles of Insect Control."

Chapter VII—Direct Control by Chemical Methods

Beal, J. A., Kimmey, J. W., and Rapraeger, E. F., 1935. Deterioration of fire killed douglas fir, *Timberman*, **37**: 12–17.

Craighead, F. C., 1915. A new mixture for controlling wood-boring insects, *Jour. Econ. Ent.*, **7**: 513.

Fracker, S. B., and Granovsky, A., 1928. Airplane dusting to control the hemlock spanworm, *Jour. Forestry*, **26**: 12–33.

Furniss, R. L., 1937. Salvage on Tillamook Burn as affected by insect activity, *Timberman*, **39**: 11–13.

Hamilton, C. C., 1937. Entoma, a directory of insect pest control, Published by the Eastern Branch, *Amer. Assn. Econ. Ent.*

———, 1938. Insecticides applied by autogiro to control cankerworms infesting forest areas, *Jour. Econ. Ent.*, **31**: 513–518.

Hang, G. W., and Peterson, Alvah, 1938. The effect of insecticides on a beneficial Coccinellid, *Hippodamis convergens* Guer., *Jour. Econ. Ent.*, **31**: 87–92.

Hartzell, F. Z., and Moore, J. B., 1937. Control of oyster-shell scale on apple by means of coal tar oils, tar-lubricating oils, and lubricating oils containing dinitro-o-cyclohexylphenol, *Jour. Econ. Ent.*, **30**: 651–655.

Kotinsky, J., 1921. Insects injurious to deciduous shade trees and their control, *U. S. Dept. Agr., Farmers' Bull.* 1169.

Moore, Wm., 1925. Electric charges of arsenical particles, *Jour. Econ. Ent.*, **18**: 282–286.

Moore, Wm., and Graham, S. A., 1918. Physical properties governing the efficacy of contact insecticides, *Jour. Agr. Res.*, **13**: 523–538.

Salman, K. A., 1938. Recent experiments with penetrating oil sprays for the control of barkbeetle, *Jour. Econ. Ent.*, **31**: 119–123.

Worthley, L. H., 1917. Solid-stream spraying against the gypsy moth, *U. S. Dept. Agr., Bull.* 480.

Chapter VIII—Indirect Control of Tree Insects

Burke, H. E., 1921. Notes on the carpenter worm and a new method of control, *Jour. Econ. Ent.*, **14**: 369–372.

Burks, B. D., Ross, H. H., and Frison, T. H., 1938. An economical portable light (Argon-mercury) for collecting nocturnal insects, *Jour. Econ. Ent.*, **31**: 316–318.

Collins, C. W., 1920. Gypsy-moth tree-banding material, *U. S. Dept. Agr., Bull.* 899.

Craighead, F. C., 1922. Experiments with spray solutions for preventing insect injury to green logs, *U. S. Dept. Agr., Bull.* 1079.

Graham, S. A., 1916. Notes on the control of the white-pine weevil, *Jour. Econ. Ent.*, **9**: 549–551.

———, 1922. Some entomological aspects of the slash-disposal problem, *Jour. Forestry*, **20**: 437–447.

———, 1925. The felled tree trunk as an ecological unit, *Ecology*, **6**: 397–411.

Keen, F. P., Craighead, F. C., *et al.* 1927. The relation of insects to slash disposal, *U. S. Dept. Agr., Circ.* 411.

Miller, J. M., 1926. The western pine beetle control problem, *Jour. Forestry*, **24**: 897–910.

PEIRSON, H. B., 1921. The life history and control of the Pales weevil, *Harvard Forest Bull.* 3.

PETTIT, R. H., 1923. A successful repellent for the flat-headed borer, *Mich. State Bd. Agr., Rept.* **62**: 219–235.

PRESTON, J. F., 1925. Control of bark beetles on the national forests, *Jour. Forestry*, **23**: 49–61.

SNYDER, T. E., 1921. White ant-proof wood for the tropics, *Jour. Econ. Ent.*, **14**: 496–501.

———, 1924. Tests of methods of protecting woods against termites, *U. S. Dept. Agr., Bull.* 1231.

———, 1926. Preventing damage by lyctus powder-post beetles, *U. S. Dept. Agr., Farmers' Bull.* **1477**: 1–13.

Chapter IX—Other Indirect Control Methods

BAIRD, A. B., 1937. Biological control of the spruce sawfly, *Diprion polytomum, Pulp Paper Mag. Can.*, March, 1937.

BALCH, R. E., 1934. Cultural practices and forest insects, *Sep. 65th Ann. Rep. Ent. Soc. Ontario.*

BEHRE, C. E., CLINE, A. C., and BAKER, W. L., 1936. Silvicultural control of the gypsy moth, *Mass. Forest Park Assn., Bull.* 157.

BURGESS, A. F., 1926. The present status of the control of the gypsy moth and brown-tail moth by means of parasites, *Jour. Econ. Ent.*, **19**: 289–294.

BURGESS, A. F., and COLLINS, C. W., 1915. The calosoma beetle, *U. S. Dept. Agr., Bull.* 251.

CHAPMAN, R. N., 1915. Observations on the life history of *Agrilus bilineatus, Jour. Agr. Res.*, **3**: 283–294.

CLEMENT, G. E., and MUNRO, W., 1917. Control of the gypsy moth by forest management, *U. S. Dept. Agr., Bull.* 484.

COLLINS, C. W., 1936. Observations on a recurring outbreak of *Heterocampa guttivitta* and natural enemies controlling it, *Jour. Agr. Res.*, **32**: 689–699.

CRAIGHEAD, F. C., 1919. Protection from the locust borer, *U. S. Dept. Agr., Bull.* 787.

———, 1925. Relation between the mortality of trees attacked by spruce budworm and previous growth, *Jour. Agr. Res.*, **30**: 541–555.

DUNNING, DUNCAN, 1928. A tree classification for the selection forests of the Sierra Nevada, *Jour. Agr. Res.*, **36**: 755–770.

EVENDEN, J. C., 1938. An instance of insect damage resulting from zero-margin selective cutting of ponderosa pine, *Appl. For. Notes, Northern Rocky Mt. Range Exp. Sta.*, 84.

GRAHAM, S. A., 1926. Biology and control of the white-pine weevil, *Cornell Agr. Exp. Sta., Bull.* 449.

———, 1928. The influence of small mammals and other factors upon larch sawfly survival, *Jour. Econ. Ent.*, **21**: 301–310.

———, 1938. Relation of insects to primitive and present-day forests, *Jour. Forestry*, **36**: 908–1004.

GRAHAM, S. A., and BAUMHOFER, L. G., 1927. The pine tipmoth in Nebraska National Forest, *Jour. Agr. Res.*, **35**: 323–333.

——— and ——— 1928. Susceptibility of pines to tipmoth injury (*in manuscript*).

HALL, R. C., 1933. Post-logging decadence of northern hardwoods, *Univ. Mich., School Forestry Cons., Bull.* 3.

HARTLEY, CARL, 1927. Forest genetics with particular reference to disease resistance, *Jour. Forestry*, **25**: 667–686.

HOSLEY, N. W., 1936. Norway spruce in the northeastern United States, *Harvard Forest Bull.*, 19.

HOWARD, L. O., 1926. The parasite element of natural control of injurious insects, *Jour. Econ. Ent.*, **19**: 271–282.

———, 1922. A side line on the importation of insect parasites of injurious insects, *Proc. Nat. Acad. Sci.*, June, 1922.

KEEN, F. P., 1936. Relative susceptibility of ponderosa pine to bark-beetle attack, *Jour. Forestry*, **34**: 919–927.

MOSHER, F. H., 1915. Food plants of the gypsy moth, *U. S. Dept. Agr., Bull.* 250.

ORR, L. W., 1931. Studies on natural vs. artificial control of the pine tortoise scale, *Univ. Minn. Agr. Exp. Sta., Tech. Bull.* 79.

PEMBERTON, C. E., and WILLARD, H. F., 1918. Interrelations of fruitfly parasites in Hawaii, *Jour. Agr. Res.*, **12**: 285–296.

RABER, ORAN, 1937. Water utilization of trees with special reference to the economic forest species of the North Temperate Zone, *U. S. Dept. Agr., Msc. Pub.* 257.

ROESER, JACOB, JR., 1926. The importance of seed source and the possibilities of forest-tree breeding, *Jour. Forestry*, **24**: 38–51.

STRONG, LEE A., 1938. Legislation in the United States for the control of insects and other plant diseases, *U. S. Dept. Agr., Bur. Ent. P. Q., Mimeographed paper* E-455, Oct. 11, 1938.

THOMPSON, W. R., 1923. A criticism of the "sequence" theory of parasitic control, *Ann. Ent. Soc. Am.*, **16**: 115–128.

TOTHILL, J. D., 1923. Notes on the outbreak of the spruce budworm, forest tent caterpillar, and larch sawfly in New Brunswick, *Proc. Acadian Ent. Soc.*, **1922**, no 8: 172–182.

———, 1922. The natural control of the fall webworm in Canada, *Can. Dept. Agr., Bull.* 3 (new ser.).

TRÄGÅRDH, IVAR, 1934. A new method of obtaining an accurate estimate of the number of insects infesting storm-ravaged forests, *Proc. Fifth Pacific Sci. Congress*, Victoria and Vancouver, B. C., Canada, **1933**: 3397–3404.

WARDLE, R. A., 1929. "The Problems of Applied Entomology," p. 504.

WESTVELD, MARINUS, 1930. Suggestions for the management of spruce stands in the Northeast, *U. S. Dept. Agr., Cir.* 134.

WILLARD, H. F., and MASON, A. C., 1937. Parasitization of the Mediterranean fruitfly in Hawaii, 1914–1933, *U. S. Dept. Agr., Cir.* 439.

WILLIAMS, C. B., 1918. The food of the mongoose in Trinidad, *Trinidad Tobago, Dept. Agr., Bull.* **17**: 167–186.

Chapter X—Leaf-eating Insects

Birch Leaf-mining Sawfly, *Fenusa pumila* Klug:
FRIEND, R. B., 1933. *Conn. Agr. Exp. Sta., Bull.* 348.
PEIRSON, H. B., 1936. Biology and control, *Maine Forest Service, Bull.* 11.
Birch-leaf Skeletonizer, *Bucculatrix canadensisella* Chamb.:
FRIEND, R. B., 1927. *Conn. Agr. Exp. Sta., Bull.* 288.
LINTNER, J. A., 1893. Insects of New York, *8th Rept.*, 133–140, 1891.
Black-walnut Caterpillar, *Datana integerrima* Grote and Rob.:
FELT, E. P., 1905. *New York State Museum, Memoir* **8**: 303–305.
Brown-tail Moth, *Nygmia phaeorrhoea* (Donv.):
BRITTON, W. E., 1914. *Conn. Agr. Exp. Sta., Bull.* 182.
———, *et al.*, 1919. *Conn. State Ent. Rept., Bull.* **211**: 272–290.
BURGESS, A. F., 1917. *U. S. Dept. Agr., Farmers' Bull.* 845.
California oak worm, *Phryganidia californica* Pack.:
BURKE, H. E., and HERBERT, F. B., 1920. *U. S. Dept. Agr., Farmers' Bull.* 1076.
Cankerworms:
BALCH, R. E., 1937. Effectiveness of banding, *68th Rept. Ent. Soc. Ontario.*
HARTZELL, A., and YOUDEN, W. J., 1935. Efficiency of banding, *Contrib. Boyce Thompson Inst.*, **7**: 365.
PORTER, B. A., and ALDEN, C. H., 1924. *U. S. Dept. Agr., Farmers' Bull.* 1238.
Catalpa sphinx, *Ceratomia catalpae* (Bvd.):
HOUSER, J. S., 1908. *Ohio Agr. Exp. Sta., Bull.* **332**: 238–241.
HOWARD, L. O., and CHITTENDEN, F. H., 1907. *Dept. Agr. Bur. Ent., Circ.* 96.
Cottonwood leaf-beetle, *Chrysomela scripta* (Fab.):
FELT, E. P., 1906. *New York State Museum, Mem.* **8**: 317–321.
Elm leaf-beetle, *Galerucella xanthomelaena* (Schr.):
BRITTON, W. E., 1932. *Conn. Agr. Exp. Sta., Circ.* 84.
HERRICK, G. W., 1911. *Cornell Agr. Exp. Sta., Circ.* 8.
Elm-leaf sawfly, *Kaliofenusa ulmi* (Sund.):
CHRYSTAL, R. N., 1919. *Agr. Gazette Can.*, **6**: 725–728.
SLINGERLAND, M. V., 1905. *Cornell Agr. Exp. Sta., Bull.* **233**: 51–57.
Elm spanworm, *Ennomos subsignarius* Hubn.:
FELT, E. P., 1908. *New York State Museum, Bull.* **124**: 23–28.
HERRICK, G. W., 1910. *Cornell Agr. Exp. Sta., Bull.* 286.
European-larch case-bearer, *Coleophora laricella* Hbn.:
FELT, E. P., 1933. *Jour. Econ. Ent.*, **26**: 46–47.
European spruce sawfly, *Diprion polytomum* (Htg.):
BAIRD, A. B., 1937. Biological control, *Pulp Paper Mag. Canada.*
BALCH, R. E., 1934. *Ent. Branch, Can. Dept. Agr., Special Circ.*, March, 1934.
———, 1936. *Canadian Ent.*, **LXVIII**: 23–31.
———, 1938. *Woodlands Sections, Can. Pulp Paper Assn.*, Montreal (Unnumbered.)

MacAloney, H. J., 1936. *Jour. Forestry*, **34**: 125–127.
Peirson, H. B., 1936. *Maine Forest Service, Circ.* 3.
Evergreen bagworm, *Thyridopteryx ephimeraeformis*, Haw.:
Howard, L. O., and Chittenden, F. H., 1916. *U. S. Dept. Agr. Bur. Ent., Farmers' Bull.* 701.
Fall webworm, *Hyphantria cunea* (Dru.):
Tothill, J. D., 1922. *Can. Dept. Agr., Tech. Bull.* **3**: 3–107.
Forest tent-caterpillar, *Malacosma disstria* Hubn.:
Houser, J. S., 1918. *Ohio Agr. Exp. Sta., Bull.* **332**: 241–244.
Slingerland, M. V., 1899. *Cornell Agr. Exp. Sta., Bull.* **170**: 557–564.
Swaine, J. M., 1913. *Can. Dept. Agr., Ent. Branch, Circ.* 1.
Green fruit-worm, *Gryptolitha antennata* (Walker):
Felt, E. P., 1912. *New York State Museum, Bull.* **155**: 48–52.
Green striped-maple worm, *Anisota rubicunda*, (Fabr.):
Howard, L. O., and Chittenden, F. H., 1909. *U. S. Dept. Agr. Bur. Ent., Circ.* 110.
Gypsy moth, *Porthetria dispar* (L.):
Behre, C. E., Cline, A. C., and Baker, W. L., 1936. Silvicultural control, *Mass. Forest Park Assn., Bull.* 157.
Burgess, A. F., 1917. *U. S. Dept. Agr., Farmers' Bull.* 845.
Burgess, A. F., and Baker, W. L., 1938. *U. S. Dept. Agr., Circ.* 464.
Collins, C. W., 1915. *U. S. Dept. Agr., Bull.* 273.
Fiske, W. F., 1913. *U. S. Dept. Agr., Bur. Ent. P. Q., Circ.* 164.
Hemlock looper, *Ellopia fiscellaria* Guen.:
Dibble, C. B., 1926. *Mich. Quart. Bull.*, **8**: 145–148.
Fracker, S. B., and Granovski, A., 1927. *Jour. Econ. Ent.*, **20**: 287–295.
Hopping, G. R., 1934. *Sci. Agr.*, **15**: 12–29.
Larch case-bearer, *Coleophora laricella* Hubn.:
Britton, W. E., 1924. *Conn. Agr. Exp. Sta., Bull.* **256**: 288–291.
Herrick, G. W., 1912. *Jour. Econ. Ent.*, **5**: 172.
Larch sawfly, *Pristiphora erichsonii* (Hart):
Hewitt, C. G., 1912. *Can. Dept. Agr., Ent., Branch, Bull.* 10.
Locust leaf-miner, *Chalepus dorsalis* Thunb.:
Dominick, C. B., 1938. *Jour. Econ. Ent.*, **31**: 186–189.
Lodgepole needle-miner, *Recurvaria milleri* Busck.:
Patterson, J. E., 1921. *Jour. Agr. Res.*, **21**: 127–142.
Maple leaf-cutter, *Paraclemensia acerifoliella* (Fitch):
Herrick, G. W., 1923. *Cornell Agr. Exp. Sta., Bull.* 417.
Mourning-cloak butterfly, *Aglais* (*Euvanessa*) *antiopa* (Linn.):
Felt, E. P., 1906. *New York State Museum, Mem.* **8**: 158–162.
Orange-striped oak-worm, *Anisota senatoria* (Abb. and Sm.):
Hauser, J. S., 1918. *Ohio Agr. Exp. Sta., Bull.* **332**: 249–251
Pandora moth, *Coloradia pandora* Blake:
Burke, H. E., 1932. *U. S. Dept. Agr., Circ.* 224.
Eldredge, D. F., 1923. *Am. For.*, **254**: 330–332.
Miller, J. M., 1928. *Nature*, Nov., 1928.
Pine butterfly, *Neophasia menapia* Felder:
Evenden, J. C., 1924. *Timberman*, p. 54, May, 1924.

———, 1926. *Jour. Agr. Res.*, **33**: 339–344.
JONES, U., and SCHMITZ, H. 1923. *Timberman*, pp. 156–157, Jan. 1923.
Pine sawflies:
GRAHAM, S. A., 1925. *Jour. Econ. Ent.*, **18**: 337–345.
MIDDLETON, WM., 1921. *Jour. Agr. Res.*, **20**: 741–760.
———, 1922. *U. S. Dept. Agr., Farmers' Bull.* 1259.
———, 1923. *U. S. Dept. Agr., Farmers' Bull.* 1182.
Satin moth, *Stilpnotia salicis* (Linn.):
BURGESS, A. F., 1927. *U. S. Dept. Agr., Bull.* 1469.
COLLINS, C. W., 1931. *U. S. Dept. Agr., Circ.* 189.
GLENDENNING, R., 1924. *Can. Dept. Agr.*, Pamphlet 50 *n. s.*
KEEN, F. P., 1938. Insect enemies of western forests, *U. S. Dept. Agr., Msc. Pub.* 273.
Snow-white Linden-moth, see Elm spanworm.
Spruce budworm, *Cacoecia fumiferana* (Clem.):
BALCH, R. E., 1930. On lodgepole pine, *U. S. Bur. Ent. P. Q.*, Ms.
CRAIGHEAD, F. C., 1924. *Can. Dept. Agr., Bull.* 37.
GRAHAM, S. A., 1923. *Univ. Mich. Special Bull.* 68.
———, 1935. On pine, *Univ. Mich., School Forestry Cons., Bull.* 6.
GRAHAM, S. A., and ORR, L. W., 1938. The spruce budworm in Minnesota, Ms.
White-marked tussock-moth, *Hemerocampa leucostigma* Abb. and Sm.:
FELT, E. P., 1912. *New York State Museum, Bull.* **156**: 14–17.
HOUSER, J. S., 1918. *Ohio Agr. Exp. Sta., Bull.* **332**: 207–213.
RUGGLES, A. G., 1917. *Minn. State Ent., Circ.* 46.
SWAINE, J. M., 1918. *Can. Dept. Agr., Ent. Branch, Circ.* **11.**

Defoliators in general:
MCDANIEL, E. I., 1933. Deciduous trees, *Mich. State Coll. Agr. Exp. Sta., Special Bull.* 242.
———, 1932. Evergreens, *Mich. State Coll. Agr. Exp. Sta., Cir. Bull.* 141.

Chapters XI, XII, and XIII—Meristem Insects

Balsam-fir bark-beetle, *Pityokteines sparsus* Lec.:
SWAINE, J. M., 1919. *Quebec Soc. Protection Plants, Ann. Rept.*, **11**: 46–48.
Bark loosener, *Callidium antennatum* Newn.:
MILLER, J. M., 1933. Damage to yellow pine lumber, *U. S. Dept. Agr., Bur. Ent. P. Q., Berkeley Lab.*, Mimeographed, unnumbered.
Black Hills beetle, *Dendroctonus ponderosae* Hopk.:
BLACKMAN, M. W., 1931. *N. Y. State Coll. Forestry, Bull.* **IV**, no. 4.
HOPKINS, A. D., 1905. *U. S. Dept. Agr., Bur. Ent., Bull.* 56.
Black turpentine-beetle, *Dendroctonus terebrans* Oliv.:
HOPKINS, A. D., 1909. *U. S. Dept. Agr., Bur. Ent., Bull.* 83, pt. 1.
Bronze birch-borer, *Agrilus anxius* Gory:
BLACKMAN, M. W., and ELLIS, W. O., 1916. *N. Y. State Coll. Forestry, Bull.* **26**: 46–49.

Britton, W. E., 1922. *Conn. Agr. Exp. Sta., Bull.* **247**: 359–361.
Peirson, H. B., 1927. *Jour. Forestry*, **25**: 68–72.
Slingerland, M. V., 1906. *Cornell Agr. Exp. Sta., Bull.* **234**: 65–78.
Carpenter worm, *Prionoxystus robiniae* (Peck):
Burke, H. E., 1921. *Jour. Econ. Ent.*, **14**: 369–372.
Felt, E. P., 1905. *New York State Museum, Mem.* **8**: 79–84.
Packard, A. S., 1890. *Ent. Comm., Rept.* **5**: 53–58.
Cottonwood borer, *Plectrodera scalator* Fabr.:
Milliken, F. B., 1916. *U. S. Dept. Agr., Bull.* 424.
Dipterous cambium-miners:
Burke, H. E., 1905. *U. S. Dept. Agr., Bur. Ent., Circ.* 61: 1–10.
Green, C. T., 1914. *Jour. Agr. Res.*, **1**: 471–474.
Douglas-fir pitch-moth, *Synthadon novaroensis*, (Edw).:
Brunner, Josef., 1915. *U. S. Dept. Agr., Bull.* 255.
Eastern spruce-beetle, *Dendroctonus piceaperda* Hopk.:
Hopkins, A. D., 1909. *U. S. Dept. Agr., Bur. Ent., Bull.* 83, pt. 1.
Swaine, J. M., 1924. *Can. Dept. Agr., n. s. Pamphlet* 48.
Elm bark-beetle, *Hylurgopinus rufipes* (Eichhoff):
Kaston, B. J., 1939. Morphology, *Conn. Agr. Exp. Sta., Bull.* 420.
Martin, H. M., 1938. *Jour. Econ. Ent.*, **31**: 470–477.
Elm snout-beetle, *Magdalis barbita* (Say) and *M. armicollis* (Say):
Felt, E. P., 1905. *New York State Museum, Mem.* **8**: 73–75.
Hubbard, H. G., 1874. *Psyche*, **1**: 5–6.
European pine-shoot moth, *Rhyacionia buoliana* (Shiff):
Busck, August, 1915. *U. S. Dept. Agr., Bull.* **170**: 1–11.
Brunner, Joseph, 1915. *U. S. Dept. Agr., Bull.* **295**: 1–12.
Friend, R. B., and Plumb, G. H., 1938. Control, *Jour. Econ. Ent.*, **31**: 176–183.
Friend, R. B., Plumb, G. H., and Hicock, H. W., 1938. *Jour. Econ. Ent.*, **31**: 506–513.
Parr, Thaddeus, 1937. In Sweden, *Jour. Forestry*, **35**: 269–273.
Fir engraver, *Scolytus ventralis* Lec.:
Struble, G. R., 1937. *U. S. Dept. Agr., Circ.* 419.
Flat-headed apple-tree borer, *Chrysobothris femorata* Oliv.:
Brooks, F. E., 1919. *U. S. Dept. Agr., Farmers' Bull.* **1065**: 3–12.
Burke, H. E., 1919. *Jour. Econ. Ent.*, **12**: 326–330.
Hickory bark-beetle, *Scolytus quadrispinosus* Say:
Blackman, M. W., 1924. *Jour. Econ. Ent.*, **17**: 460–470.
Hopkins, A. D., 1912. *U. S. Dept. Agr., Bur. Ent., Circ.* 144.
Hickory spiral-borer, *Agrilus arcuatus* Say:
Brooks, F. E., 1926. *Jour. Agr. Res.*, **33**: 331–338.
Large pine-sawyer, *Monochamus confusor* (Kirby):
Swaine, J. M., 1917. *Ont. Ent., Soc., Rept.* **471**: 96–97.
Leopard moth, *Zeuzera pyrina* (Linn.):
Britton, W. E., and Cromie, G. A. 1911. *Conn. Agr. Exp. Sta., Bull.* **169**: 3–24.
Howard, L. O., and Chittenden, F. H. 1916. *U. S. Dept. Agr., Farmers' Bull.* 708.

Linden borer, *Saperda vestita* Say.:
FELT, E. P., and JOUTEL, L. H., 1904. *New York State Museum, Bull.* **74**: 54–58.
Locust borer, *Cyllene robiniae* (Forst.):
CRAIGHEAD, F. C., 1919. *U. S. Dept. Agr., Bull.* **787**: 1–12.
———, 1937. Drought, *Jour. Forestry*, **35**: 792–793.
GARMAN, H., 1915. *Ky. State Forester, Bien. Rept.* **2**: 3–21.
HALL, R. C., 1937. Shipmast locust, *Jour. Forestry*, **35**: 721–727.
SECREST, H. C., 1937. Environmental factors, *U. S. Dept. Agr., Bur. Ent. P. Q., For. Ins. Inv., Cent. States, For. Exp. Sta.*, Mimeographed publication, Mar. 22, 1937.
ST. GEORGE, R. A., and BEAL, J. A., 1932. *Jour. Econ. Ent.*, **25**: 713–721.
Mountain pine-beetle, *Dendroctonus monticolae* Hopk.:
CRAIGHEAD, F. C., 1925. *Jour. Forestry*, **23**: 340–354.
DELEON, D., BEDARD, W. D., and TERRELL, T. T., 1934. Biology and control, *Jour. Forestry*, **32**: 430–436.
HOPKINS, A. D., 1909. *U. S. Dept. Agr., Bur. Ent. P.Q., Bull.* 83, pt. 1.
HOPPING, RALPH, 1921. *Can. Dept. Agr., Ent. Branch, Circ.* 15.
PATTERSON, J. E., 1930. Control by solar heat, *U. S. Dept. Agr., Tech. Bull.* 195.
Nantucket pine-moth, *Rhyacionia frustrana* (Scudder):
BAUMHOFER, L. G., 1936. Preventing distribution on nursery stock, *U. S. Dept. Agr., Bur. Ent. P. Q., Mimeographed publication* E-366.
GRAHAM, S. A., and BAUMHOFER, L. G., 1927. *Jour. Agr. Res.*, **35**: 323–333.
WAKELEY, PHILIP C., 1937. *Southern For. Exp. Sta., Occasional paper* 45.
Oak-sapling borer, *Goes tesselatus* Haldman:
BROOKS, F. E., 1919. *Jour. Agr. Res.*, **26**: 313–317.
Oak twig-girdler, *Agrilus angelicus* Horn and *A. arcuatus torquatus*:
BURKE, H. E., 1920. *Jour. Econ. Ent.*, **13**: 379–384.
RUGGLES, A. G., 1919. *Minn. State Ent., Rept.* **17**: 15–20.
Pales weevil, *Hylobius pales* (Herbst):
PEIRSON, H. B., 1921. *Harvard Forest Bull.* **3**: 1–33.
Pine bark-beetle, *Ips pini* (Say).
CLEMENS, W. A., 1916. *Cornell Agr. Exp. Sta., Bull.* **383**: 287–289.
Pine pitch-mass borer, *Parharmonia pini* Kellicott:
FELT, E. P., 1905. *New York State Museum, Mem.* **8**: 341–342.
Pine pityogenes, *Pityogenes hopkinsi* Sw.:
BLACKMAN, M. W. and SWAINE, J. M., 1915. *N. Y. State Coll. Forestry, Tech. Pub.* 2.
Poplar borer, *Saperda calcarata* Say:
FELT, E. P., and JOUTEL, L. H., 1904. *New York State Museum, Bull.* **74**: 39–44.
HOFER, GEORGE, 1920. *U. S. Dept. Agr., Farmers' Bull.* **1154**: 3–11.
Red turpentine-beetle, *Dendroctonus valens* Lec.:
HOPKINS, A. D., 1909. *U. S. Dept. Agr., Bur. Ent., Bull.* 83, pt. 1.
Sequoia pitch-moth, *Vespamima sequoia* (Hy. Edw.):
BRUNNER, JOSEPH, 1914. *U. S. Dept. Agr., Bull.* 111.

Small European elm-bark-beetle, *Scolytus multistriatus* Marsham.:
COLLINS, D. L., 1938. *Jour. Econ. Ent.*, **31**: 196–200.
Southern pine-beetle, *Dendroctonus frontalis* Zimm.:
CRAIGHEAD, F. C., 1925. *Jour. Econ. Ent.*, **18**: 577–586
HOPKINS, A. D., 1920. *U. S. Dept. Agr., Farmers' Bull.* 1188.
ST. GEORGE, R. A., 1929. *U. S. Dept. Agr., Farmers' Bull.* 1586.
Strawberry-root weevil, *Brachyrhinus ovatus*, Linn.:
GAMBRELL, F. L., 1938. *Jour. Econ. Ent.*, **31**: 107–112.
MCDANIEL, E. I., 1932. *Mich. State Coll. Agr. Exp. Sta., Circ. Bull.* **141**: 42–45.
Sugar-maple borer, *Glycobius* (*Plagionotus*) *speciosus* (Say):
BRITTON, W. E., 1922. *Conn. Agr. Exp. Sta., Bull.* **247**: 351–355.
BLACKMAN, M. W., and ELLIS, W. O., 1916. *N. Y. State Coll. Forestry*, 16, **26**: 60–65.
KOTINSKI, JOCOB, 1921. *U. S. Dept. Agr., Farmers' Bull.* **1167**: 53–55.
Two-lined chestnut-borer, *Agrilus bilineatus* (Weber):
CHAPMAN, R. N., 1915. *Jour. Agr. Res.*, **3**: 283–294.
Western cedar-borer, *Trachykele blondeli* Mars.:
BURKE, H. E., 1928. *U. S. Dept. Agr., Tech. Bull.* 48.
Western pine-beetle, *Dendroctonus brevicomis* Lec.:
CHAMBERLIN, W. J., 1920. *Ore. Agr. Exp. Sta., Bull.* 172.
PATTERSON, J. E., 1927. Slash and infestation, *U. S. Dept. Agr., Tech. Bull.* 3.
White grubs, *Phyllophaga* (*Lachnosterna*):
DAVIS, J. J., 1930. *Purdue Univ., Bull.* 168.
FLEMING, W. E., BAKER, F. E., and KOBLITSKI, LOUIS, 1937. Evergreen seedlings, *Jour. Forestry*, **35**: 679–688.
FORBES, S. A., 1907. *Univ. Ill. Agr. Exp. Sta., Bull.* 116.
LUGENBILL, PHILIP, 1938. Control in cereal and forage crops, *U. S. Dept. Agr., Bull.* 1798.
ST. GEORGE, R. A., 1935. Arsenical injury to seedlings, *Jour. Forestry*, **33**: 726–728.
YEAGER, L. E., 1937. *Univ. Mich.*, Unpublished thesis on file in Univ. of Mich. Lib.
White-pine weevil, *Pissodes strobi* (Peck):
CLINE, A. C., 1931. Reclaiming weeviled plantations, *Mass. For. Assn., Bull.* 152.
———, 1933. Improvement of weeviled plantations, *Conn. For. Park Assn.*, Pub. 24.
———, and MACALONEY, H. J., 1931. Reclaiming severely weeviled pine plantations, *Mass. For. Assn., Bull.* 152.
———, 1933. Improvement of plantations, *Conn. For. Park Assn., Pub.* 24.
———, 1935. Reclamation of severely weeviled plantations, *Jour. Forestry*, **33**: 932–935.
GRAHAM, S. A., 1918. *Jour. Forestry*, **15**: 192–202.
———, 1926. *Cornell Agr. Exp. Sta., Bull.* **449**: 3–32.

Hopkins, A. D., 1907. *U. S. Dept. Agr., Bur. Ent., Circ.* **90**: 1–8.
MacAloney, H. J., 1930. *N. Y. State Col. Forestry, Tech. Pub.* 28, Vol. III, no. 1.
———, 1932. *U. S. Dept. Agr., Circ.* 221.
Peirson, H. B., 1922. *Harvard Forestry Bull.* **5**: 1–42.
White-spotted sawyer, *Monochamus scutellatus* (Say):
Tothill, J. D., 1923. *New Brunswick Land Dept., Ann. Rept.* **63**: 86–87.
Willow curculio, *Cryptorhynchus lapathi* (Linn.):
Blackman, M. W., and Ellis, W. O., 1915. *N. Y. State Coll. Forestry, Bull.* **26**: 67–71.
Matheson, Robert, 1915. *Jour. Econ. Ent.*, **8**: 522–525.
———, 1917. *Cornell Agr. Exp. Sta., Bull.* 388.
Wireworms:
Hyslop, J. A., 1916. *U. S. Dept. Agr., Farmers' Bull.* 725.
Lane, M. C., 1925. *Jour. Econ. Ent.*, **18**: 90–95.
Wood and phloem borers (general):
McDaniel, E. I., 1933. Wood borers attacking the trunk and limbs of deciduous trees and shrubs, *Mich. State Coll. Agr. Exp. Sta., Spec. Bull.* 238.
Zimmerman pine-moth, *Pinipestis zimmermani* Grote:
Felt, E. P., 1915. *New York State Museum, Bull.* **180**: 39–42.

Bark beetles in general:
Craighead, F. C., Miller, J. M., Evenedn, J. C., and Keen, F. P., 1931. Appraisal of control, *Jour. Forestry*, **29**: 1001–1018.
Forest Service Handbook, 1933. *U. S. Forest Service*, Portland, Ore., (Mimeographed. Prepared jointly by officers of U. S. For. Serv. and Bur. Ent. and P. Q.)
Johnson, P. C., 1936. Field manual of survey methods, Calif. region. Mimeographed, unnumbered. *U. S. Dept. Agr., Bur. Ent. P. Q.*, (Revised).
Keen, F. C., 1929. Barkbeetles infesting western forest trees, *U. S. Dept. Agr., Bur. Ent. P. Q.*, Mimeographed, unnumbered. (Revised.)
Miller, J. M., and Patterson, J. E., 1927. Fire and beetle attack, *Jour. Agr. Res.*, **34**: 597–613.

Chapter XIV—Wood Destroyers

Ambrosia beetles:
Felt, E. P., 1905. *New York State Museum, Mem.* **8**: 289–293.
Hopkins, A. D., 1905. *U. S. Dept. Agr. Bur. Ent., Circ.* **82**: 1–4.
Hubbard, H. G., 1897. *U. S. Dept. Agr. Div. Ent., n. s. Bull.* 7.
Buprestid dry-wood borer, *Chrysophana placida* Lec.:
Burke, H. E., 1917. *Jour. Econ. Ent.*, **10**: 406–407.
Carpenter ant, *Camponotus pennsylvanicus* (Degeer):
Comstock, J. H., 1915. "Manual for the Study of Insects."
Friend, R. B., and Carlson, A. B., 1937. Control in telephone poles, *Conn. Agr. Exp. Sta., Bull.* 403.
Graham, S. A., 1918. *Minn. State Ent., Rept.* **17**: 32–40.

Wheeler, W. M., 1910. "Ants: Their Structure, Development, and Behavior."

Carpenter bee, *Xylocopa orpifix* Smith:

Nininger, H. H., 1916. *Jour. Ent., and Zoöl.*, **8**: 157–166.

Horntails:

Felt, E. P., 1905. *New York State Museum, Mem.* **8**: 667–669.

Harrington, W. H., 1883. *Ont. Ent. Soc., Rept.* **14**: 40–42.

Riley, C. V., 1888. *Insect Life*, **1**: 168–179.

Marine borers:

Bartsch, Paul, 1922. *Smith. Inst. U. S. Nat. Mus., Bull.* 122.

Calman, W. T., 1919. *Br. Museum (Nat. Hist.), Econ. Ser.* 10.

Dove, W. H., and Miller, R. C., 1923. *Univ. Cal. Pub. Zoöl.*, **22**: 383–400.

Hill, C. L., and Kofoid, C. A., 1927. San Francisco Bay marine piling committee rept. *Nat. Res. Council* and *Amer. Wood Preservers Assn.* (Unnumbered.)

Miller, R. C., and Boynton, L. C., 1926. *Science, n. s.* **63**: 524.

Sigerfoos, C. P., 1907. *U. S. Bur. Fish., Bull.* **27**: 191–231.

Smith, S. C., 1907. *U. S. Dept. Agr., Forest Serv., Circ.* **128**: 3–15.

Parandra borer, *Parandra brunnea* Fabr.:

Brooks, F. E., 1915. *U. S. Dept. Agr., Bull.* **262**: 1–7.

Snyder, T. E., 1910. *U. S. Dept. Agr., Bur. Ent., Bull.* **94**: 1–11.

———, 1911. *U. S. Dept. Agr., Bur. Ent., Circ.* 134.

Powder-post beetles:

Blake, E. G., 1925. "Enemies of Timber: Dry Rot and the Death-watch Beetle."

Snyder, T. E., 1916. *Jour. Agr. Res.*, **6**: 273–276.

———, 1926. *U. S. Dept. Agr., Farmers' Bull.* **1477**: 1–12.

Termites, Isoptera:

Banks, Nathan, and Snyder, T. E., 1920. Taxonomy, biology, and distribution, *Smithsonian Inst., U. S. Nat. Mus., Bull.* 108.

Emerson, A. E., 1926. Development of soldiers, *Zoologica (N. Y. Zool. Soc.)*, **7**: 69–100.

Hunt, George M., and Snyder, T. E., 1936. Exposure test, *Seventh Progress Rept., 32nd Ann. Meeting, Amer. Wood Preservers' Assn.*

Kofoid, C. A., (ed.) and others, 1934. "Termites and Termite Control," University of California Press.

McCauley, W. E., and Flint, W. P., 1938. In Illinois, *Ill. Nat. Hist. Surv., Circ.* 30.

Snyder, T. E., 1926. Biology of termite castes, *Quart. Rev. Biol.*, **1**: 522–552.

———, 1933. Injury to buildings, *U. S. Dept. Agr., Leaflet* 101.

———, 1934. *U. S. Dept. Agr., Farmers' Bull.* 1472.

———, 1935. "Our Enemy the Termite," Comstock Pub. Co.

Turner, N., and Townsend, J. F., 1936. Control, *Conn. Exp. Sta., Bull.* 382.

Turpentine borer, *Buprestis apricans* Herbst:

Beal, J. A., 1932. *U. S. Dept. Agr., Circ.* 226.

Western cedar-borer, *Trachykele blondeli* Mars.:
BURKE, H. E., 1928. *U. S. Dept. Agr., Tech. Bull.* 48.
HOPPING, G. R., 1932. *Can. Ent.*, **64**: 189–190.

Chapter XV—Sap-sucking Insects

Adelgids:
CHRYSTAL, R. N., 1916. *Ont. Ent. Soc., Rept.* **1916**: 123–130.
———, 1922. *England Forestry Comm., Bull.* 4.
GAMBRELL, F. L., 1934. Control in plantations, *N. Y. Agr. Exp. Sta., Bull.* 225.
HERRICK, G. W., and TANAKA, T., 1926. *Cornell Agr. Exp. Sta., Bull.* 454.
MACALONEY, H. J., 1935. The balsam woolly aphid in the Northeast, *Jour. Forestry*, **33**: 481–484.
WILFORD, B. H., 1937. *Univ. Mich., School Forestry Cons., Circ.* 2.
Aphids:
JONES, T. H., and GILLETTE, C. P., 1918. *Jour. Agr. Res.*, **14**: 577–593.
PATCH, E. M., 1915. *Maine Agr. Exp. Sta., Bull.* 241.
———, 1920. *Ann. Ent. Soc. Am.*, **13**: 156–167.
———, 1923. *Maine Agr. Exp. Sta., Bull.* 313.
Lacebugs:
BARBER, H. G., and WEISS, H. B., 1922. *N. J. Dept. Agr., Bur. Stat. Insp., Circ.* **54**: 3–21.
DRAKE, C. J., 1922. *New York State Coll. Forestry, Tech. Pub.* **16**: 111–116.
WADE, OTIS, 1917. *Okla. Agr. Exp. Sta., Bull.* 116.
Periodical cicada, *Magicicada septendecim:*
FELT, E. P., 1905. *New York State Museum, Mem.* **8**: 231–237.
MARLATT, C. L., 1907. *U. S. Dept. Agr. Bur. Ent., Bull.* **71**: 5–181.
Plant bugs:
BAILEY, H. L., 1920. *Vt. Com. Agr.*
FELT, E. P., 1905. *New York State Museum, Mem.* **8**: 239–240.
LINTNER, J. A., 1895. Insects of N. Y., *Rept.* **10**: 432–439.
Scale insects:
BLACKMAN, M. W., and ELLIS, W. O., 1916. Cottony maple-scale, *New York State Coll. Forestry, Bull.* **16**: 26–107.
COMSTOCK, J. H., 1883. *Cornell Agr. Exp. Sta., Second Rept.*
DOZIER, H. L., 1925. Obscure scale, *Fla. State Plant Bd., Quart. Bull.* **9**: 129–133.
GILLETTE, C. P., and LANGFORD, G. S., 1925. *Colo. State Ent., Circ.* 46.
GLENN, P. A., 1920. *Jour. Econ. Ent.*, **13**: 173.
GRISWOLD, G. H., 1925. Oyster-shell scale, *Cornell Agr. Exp. Sta., Mem.* 93.
HERBERT, F. B., 1920. Cyprus bark-scale, *U. S. Dept. Agr., Bull.* 838.
———, 1924. European elm-scale, *U. S. Dept. Agr., Bull.* 1223.
HOUGH, W. S., 1925. Comstock's mealybug, *Va. Agr. Exp. Sta., Tech. Bull.* 29.

QUAINTANCE, A. L., and SASSCER, E. R., 1910. Oyster-shell scale, *U. S. Dept. Agr., Bur. Ent., Circ.* 121.

Chapter XVI—Parasites

ALLEN, H. W., 1925. The biology of the red-tailed tachinid fly, *Miss. Agr. Exp. Sta., Bull.* 12.

BALDUFF, W. V., 1926. The bionomics of *Dinocampus coccinellae*, *Ann. Ent. Soc. Am.*, **19**: 465–498.

BURRELL, R. W., 1931. *Dexia ventralis* Aldrich, an imported parasite of the Japanese beetle, *Jour. Res.*, **43**: 323–336.

CHAPMAN, J. W., and GLASER, R. W., 1916. Further studies on wilt of gypsy-moth caterpillars, *Jour. Econ. Ent.*, **9**: 149–163.

CLAUSEN, C. P., *et al.* 1927. Parasites of *Popillia Japonica* in Japan and Chosen and their introduction into the United States, *U. S. Dept. Agr., Bull.* 1429.

COLLINS, C. W., and HOOD, C. E., 1920. Life history of *Eubiomyia calosoma*, a tachinid parasite of calosoma beetles, *Jour. Agr. Res.*, **18**: 483–498.

CRIDDLE, N., 1924. Two problems in natural control, *Ont. Ent. Soc., Ann. Rept.* **54**: 16–18.

CROSSMAN, S. S., 1922. *Apanteles melanoscelus*, an imported parasite of the gypsy moth, *U. S. Dept. Agr., Bull.* 1028.

CULVER, J. J., 1919. A study of *Compsilura concinnata*, an imported tachnid parasite, *U. S. Dept. Agr., Bull.* 766.

DOWDEN, P. B., 1933. *Lydella nigripes* and *L. piniariae*, fly parasites of certain tree-defoliating caterpillars, *Jour. Agr. Res.*, **46**: 963–995.

FISKE, W. F., 1903. A study of the parasites of the American tent-caterpillar, *N. H. State Coll. Agr. Exp. Sta., Tech. Bull.* 6.

GLASER, R. W., 1918. A new bacterial disease of gypsy-moth caterpillars, *Jour. Agr. Res.*, **13**: 515–532.

———, 1925. Specificity of bacterial diseases, *Jour. Econ. Ent.*, **18**: 769–771.

———, 1927. Studies of polyhedral diseases of insects, *Ann. Ent. Soc. Am.*, **20**: 319–342.

GRAHAM, S. A., 1918. An interesting habit of a wax-moth parasite, *Ann. Ent. Soc. Am.*, **11**: 175–180.

HEWITT, C. G., 1912. The large larch sawfly, *Can. Dept. Agr., Branch, Ent. Bull.* 10.

HOWARD, L. O., 1897. A study in insect parasitism, *U. S. Dept. Agr., Div. Ent., Bull.* 5.

JONES, T. H., WEBBER, R. T., and DOWDEN, P. B., 1938. Effectiveness of imported insect enemies of the satin moth, *U. S. Dept. Agr., Circ.* 459.

MUESEBECK, C. F. W., 1931. *Monodontomerus aereus* Walker, both a primary and secondary parasite of the browntail moth and gypsy moth, *Jour. Agr. Res.*, **43**: 445–460.

MUESEBECK, C. F. W., and DOHANIAN, S. M., 1927. A study in hyperparasitism, *U. S. Dept. Agr., Bull.* 1487.

MUESEBECK, C. F. W., and PARKER, D. L., 1933. *Hypsoter disparis* Viereck, an introduced ichneumonid parasite of the gypsy moth, *Jour. Agr. Res.*, **46**: 335–347.

PARKER, D. L., 1933. The interrelation of two hymenopterous, egg parasites of the gypsy moth, with notes on the larval stages of each, *Jour. Agr. Res.*, **46**: 23–24.

———, 1935. *Apanteles solitarius* Ratz., an introduced braconid parasite of the satin moth, *U. S. Dept. Agr., Tech. Bull.* 477.

———, 1936. *Chrysis shanghaiensis* Smith, a parasite of the oriental moth, *Jour. Agr. Res.*, **52**: 449–458.

PEMBERTON, C. E., and WILLARD, H. F., 1918. A contribution to the biology of fruit-fly parasites in Hawaii, *Jour. Agr. Res.*, **15**: 419–466.

PETERSON, ALVAH, 1930. A biological study of *Trichogramma minutum* Riley, as an egg parasite of the oriental fruit moth, *U. S. Dept. Agr., Tech. Bull.* 215.

PROPER, A. B., 1931. *Eupteromalus nitidans*, a parasite of the browntail and satin moths, *Jour. Agr. Res.*, **43**: 37–56.

———, 1934. Hyperparasitism in the case of some introduced lepidopterous tree defoliators, *Jour. Agr. Res.*, **48**: 359–376.

SHELFORD, V. E., 1926. The relation of parasites to weather conditions, *Jour. Econ. Ent.*, **19**: 283–289.

SPEARE, A. J., 1920. Further studies of *Sorosporella uvella*, *Jour. Agr. Res.*, **18**: 399–440.

ST. GEORGE, R. A., 1924. A beetle predacious on powder-post beetles, *Jour. Agr. Res.*, **29**: 49–56.

WEBBER, R. T., and SCHAFFNER, J. V., 1926. Host relations of *Compsilura concinnata* Meigen, *U. S. Dept. Agr., Bull.* 1363.

WHITE, G. F., 1924. Cutworm septicemia, *Jour. Agr. Res.*, **26**: 487–495.

Chapter XVII—Predators

BURGESS, A. F., and COLLINS, C. W., 1917. The genus Calosoma, *U. S. Dept. Agr., Bull.* 417.

BURLEIGH, T. D., 1938. The relation of birds to the establishment of longleaf pine seedlings in Southern Miss., *Southern For. Exp. Sta., Occ. paper* 75.

DUSTAN, A. G., 1923. The natural control of the white-marked tussock-moth, *Proc. Acadian Ent., Soc.*, **8**: 109–126.

FORBES, S. A., 1882. The regulative action of birds upon insect oscillations, *Ill. State Lab. Nat. Hist., Bull.* 6.

GRAHAM, S. A., 1930. Ornithology and forest entomology, *Mich. Acad. Sci., Arts, and Letters*, **XI**: 389–397.

HOPKINS, A. D., 1899. Preliminary report on insect enemies of forests in the Northwest, *U. S. Dept. Agr., Div. Ent., Bull.* **21**: 13–15.

MCATEE, W. L., 1925. The role of vertebrates in the control of insect pests, *Smithsonian Inst. Rept.*, pp. 415–437.

———, 1926. The relation of birds to woodlots in New York State, *Roosevelt Wild Life Forest Exp. Sta., N. Y. State Coll. Forestry*, **4**: 1–154.

———, 1931. Local bird refuges, *U. S. Dept. Agr., Farmers' Bull.* **1644.**

Quayle, H. J., 1911. The black scale, *Cal. Agr. Exp. Sta., Bull.* 223.

Ross, W. A., 1918. Some ladybird beetles destructive to plant lice, *Agr. Gazette Can.*, **5**: 344–347.

Smith, H. S., 1922. Report of the bureau of pest control, *Cal. Dept. Agr., Bull.* **11**: 793–838.

Smith, R. C., 1922. The biology of the Chrysopidae, *Cornell Agr. Exp. Sta., Memoir* 58.

Strickland, E. H., 1928. Can birds hold injurious insects in check?, *Sci. Mthly.*, **XXVI**: 48–56.

Tothill, J. D., 1919. Some notes on the natural color of the oyster-shell scale, *Bull. Ent. Res.*, **9**: 183–196.

———, 1922. The natural color of the fall webworm, *Can. Dept. Agr., Tech. Bull.* **3**: 2–107.

Chapter XVIII—Other Relations of Forest Insects

Collins, C. W., 1938. Two elm scolytids in relation to areas infested with the Dutch elm-disease fungus, *Jour. Econ. Ent.*, **31**: 192–195.

Craighead, F. C., 1928. Interrelation of tree-killing barkbeetles and blue stains, *Jour. Forestry* **26**: 886–887.

Felt, E. P., 1935. Barkbeetles and the Dutch elm-disease, *Jour. Econ. Ent.*, **28**: 231–236.

Fransen, J. J., 1932. Die Kleine Iepenspintkever, *Scolytus* (*Eccoptogaster*) *multistriatus* als Verbreider der Iepenziekte, *Tijdschrift over Plantenziekten*, **38e**: 197–209.

Gravatt, G. F., and Posey, G. B., 1918. Gypsy-moth larvae as agents in dissemination of the white-pine blister-rust, *Jour. Agr. Res.*, **12**: 459–462.

Leach, J. G., Orr, L. W., and Christiensen, C., 1934. Interrelationships of barkbeetles and blue-staining fungi in felled Norway Pine timber. *Jour. Agr. Res.*, **49**: 315–341.

———, ———, and ———, 1937. Further studies of interrelationship of insects and fungi in deterioration of felled Norway pine logs, *Jour. Agr. Res.*, **55**: 129–140.

Nelson, R. M., 1934. Effect of bluestain fungi on southern pines attacked by barkbeetles, *Pathologische Zeitschrift*, **7**: 327–353. (In English.)

Ruggles, A. G., 1913. Chestnut blight and insects, *Science* **38**: 852.

Rumbold, Caroline, 1931. Two blue-staining fungi associated with barkbeetle infestation of pine, *Jour. Agr. Res.*, **43**: 847–873.

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